
Dual nomenclature in organic-walled dinoflagellate cysts II: *Spiniferites elongatus* and *S. membranaceus*, and their equivalent non-fossil species *Gonyaulax ovum* comb. nov. and *G. lewisiae* sp. nov.

Head Martin J. ^{1,*}, Mertens Kenneth ², Fensome Robert A. ³

¹ Department of Earth Sciences, Brock University, St. Catharines, Ontario, Canada

² Ifremer, LITTORAL, F-29900 Concarneau, France

³ Natural Resources Canada, Geological Survey of Canada (Atlantic), Bedford Institute of Oceanography, Dartmouth, Nova Scotia, Canada

* Corresponding author : Martin J. Head, email address : mjhead@brocku.ca

Abstract :

The cyst-defined extant *Spiniferites elongatus* Reid 1974 and *Spiniferites membranaceus* (Rossignol 1964) Sarjeant 1970 are environmentally significant fossil-species of the Quaternary, the former often dominating polar and subpolar assemblages. Following cyst incubation experiments and the establishment of cultures, these species were emended to incorporate information on their motile stages, and transferred to the non-fossil genus *Gonyaulax* Diesing 1866, as *Gonyaulax elongata* (Reid 1974) Ellegaard et al. 2003 and *Gonyaulax membranacea* (Rossignol 1964) Ellegaard et al. 2003. This unified approach to dinoflagellate nomenclature severs an important link with the fossil-genus *Spiniferites* Mantell 1850. We have applied dual nomenclature, as sanctioned by the International Code of Nomenclature for algae, fungi and plants, in returning these species to their previous assignments as *Spiniferites elongatus* and *Spiniferites membranaceus*, and we propose *Gonyaulax ovum* (Gaarder 1954) comb. nov., emend. and *Gonyaulax lewisiae* sp. nov., respectively, as their equivalent non-fossil species. A distinctive morphotype initially described as *Rottneusia ampicavata* var. *ampicavata* Dobell and Norris in Harland et al. 1980 is proposed as *Spiniferites elongatus* forma *ampicavata* stat. nov.

Keywords : Dinocyst, taxonomy, dual nomenclature, *Gonyaulax ovum*, *Gonyaulax lewisiae*, *Spiniferites elongatus*, *Spiniferites membranaceus*

46
47 **43 1. Introduction**
48

49 44 Researchers in the 1960s realized that a species defined by a fossil dinoflagellate cyst
50
51 45 might represent part of the life cycle of a previously described non-fossil (usually motile-
52
53
54 46 stage-defined) species, allowing it potentially to have two names – i.e. that dual
55
56
57
58
59
60

1
2
3 47 nomenclature applied. While a single species ideally should bear just one name
4
5 48 (Ellegaard et al. 2018), the difficulties of adhering to this principle for the dinoflagellate
6
7 49 cyst record has long been anticipated (Evitt and Davidson 1964, p. 10–11; Evitt 1970, p.
8
9 50 38) and the benefits of maintaining dual nomenclature persuasively set out (Reid 1974).

11
12 51 The application of dual nomenclature largely derives from the fact that living and
13
14 52 fossil dinoflagellates (nearly always the cyst) are classified according to different species
15
16 53 concepts (Head et al., submitted). Its use provides a practical solution to the difficulties
17
18 54 of integrating extinct cyst-defined species within non-fossil genera. It allows, for
19
20 55 example, the fossil-genera *Spiniferites* Mantell 1850 and *Impagidinium* Stover and Evitt
21
22 56 1978 to coexist with the non-fossil genus *Gonyaulax* Diesing 1866, even though species
23
24 57 of *Gonyaulax* produce cysts morphologically assignable to *Spiniferites* or *Impagidinium*,
25
26 58 among others. The International Code of Nomenclature for algae, fungi and plants (ICN,
27
28 59 Turland et al. 2018), which governs the naming of dinoflagellate taxa, permits fossil- and
29
30 60 non-fossil taxa to bear separate names even when they are subsequently shown to be
31
32 61 assignable within the life-cycle of a single species (Head et al. 2016). Many species
33
34 62 names have been linked in this way.

35
36 63 However, not all modern cyst morphotypes have been integrated into a fossil cyst
37
38 64 classification scheme, and so lack fossil names. Others have hybridized names, such as
39
40 65 when a fossil-species is assigned to a non-fossil genus, or vice versa. These names give
41
42 66 rise to conceptual and practical difficulties, solutions for which have been proposed in
43
44 67 Head et al. (submitted).

45
46 68 Two such hybridized names are *Gonyaulax elongata* (Reid 1974) Ellegaard et al.
47
48 69 2003 and *Gonyaulax membranacea* (Rossignol 1964) Ellegaard et al. 2003, both
49
50
51
52
53
54
55
56
57
58
59
60

1
2
3 70 representing fossil-species assigned to a non-fossil genus. We return both species to their
4
5 71 previous assignments as *Spiniferites elongatus* Reid 1974 and *Spiniferites membranaceus*
6
7
8 72 (Rossignol 1964) Sarjeant 1970 and clarify their taxonomic and nomenclatural histories
9
10 73 and biological affinities. We then propose *Gonyaulax ovum* (Gaarder 1954) n. comb.,
11
12 74 emend. and *Gonyaulax lewisiae* n. sp., respectively, as the equivalent non-fossil species
13
14
15 75 in accordance with the practice of dual nomenclature.

16
17 76 *Gonyaulax ovum* (as *Pterosperma ovum*) was initially treated by Gaarder (1954)
18
19 77 as a prasinophycean species. Her drawings nonetheless show a dinoflagellate cyst with a
20
21 78 morphology assignable to *Spiniferites elongatus*. This species, based on non-fossil
22
23
24 79 specimens collected from the water column, therefore has a complex nomenclatural
25
26 80 history which is described in detail below.

27
28 81

29
30 82

31
32
33 83 **2. *Gonyaulax ovum* (Gaarder 1954) n. comb., emend. and *Spiniferites elongatus* Reid**
34
35 84 **1974**

36
37 85

38
39
40 86 In 1954, Karen Gaarder published the names of eight new species of phytoplankton
41
42 87 based on preserved net haul and pump samples collected during the 1910 “Michael Sars”
43
44 88 expedition (Gaarder, 1954). One of these new species, *Pterosperma ovum* Gaarder 1954
45
46
47 89 (Figure 1), was recorded from Stations 1 (49° 27' N; 8° 36' W, south of Ireland), 3 (49°
48
49 90 32' N; 10° 49' W, also south of Ireland) and 12 (43° 11' N; 9° 26' W, off Cape
50
51 91 Finisterre, Spain), being very common in all samples from Station 3, the type locality.
52
53
54
55
56
57
58
59
60

1
2
3 92 Gaarder assigned *Pterosperma ovum* to the genus *Pterosperma* Pouchet 1893 –
4
5 93 presumably a phycoma, on account of its oval central body and septa covering the
6
7 94 surface – within the family Pterospermataceae Lohmann 1904. *Pterosperma* is now
8
9 95 placed within the prasinophyte order Pyramimonadales Chadeffaud 1950 (Adl et al.
10
11 96 2019). The original description of *Pterosperma ovum* is not particularly informative but
12
13 97 Gaarder presciently noted that the species most closely resembles *Hystrichosphaera*
14
15 98 *ramosa* (Ehrenberg 1837) Deflandre 1937, now *Spiniferites ramosus* (Ehrenberg 1837)
16
17 99 Mantell 1854. Her line drawings, however, are much more revealing as they show the
18
19 100 unmistakable morphology of the dinoflagellate cyst now known as *Spiniferites*
20
21 101 *elongatus*. The specimen in Gaarder's fig. 9b (Figure 1b) shows a thick endospore and
22
23 102 cell contents as well as the characteristic outline of *Spiniferites elongatus* with trifurcate
24
25 103 processes extended at both poles, where they are connected by high septa. Unlike
26
27 104 *Spiniferites elongatus*, which was described as a fossil, *Pterosperma ovum* was collected
28
29 105 from the water column, is illustrated with cell contents, and is indisputably not a fossil.

30
31 106 *Spiniferites elongatus* Reid 1974 (Plate 1) was described from modern sediments
32
33 107 around the UK and placed within a cyst-based classification. P.C. Reid (1974) was in
34
35 108 fact an important early advocate of dual nomenclature. *Spiniferites elongatus* is a
36
37 109 distinctive species, restricted presently to the Northern Hemisphere (Zonneveld et al.
38
39 110 2013) where it is an important indicator of cold water conditions in polar and subpolar
40
41 111 settings (de Vernal et al. 2020). It has elevated abundances today off southern Ireland (as
42
43 112 independently reported by Gaarder 1954 for her *Pterosperma ovum*) and the north-
44
45 113 central North Atlantic (Zonneveld et al. 2013). Wall and Dale (1968) illustrated a cyst
46
47 114 from marine sediments at Woods Hole, Massachusetts which they referred to as
48
49
50
51
52
53
54
55
56
57
58
59
60

1
2
3 115 “*Hystrichosphaera* n. sp.” (Wall and Dale 1968, pl. 1, fig. 16). This specimen had been
4
5 116 germinated to produce a motile cell referable to *Gonyaulax* sp. Wall and Dale (1968, p.
6
7 117 271) remarked upon the similarity between their “*Hystrichosphaera* n. sp.” and
8
9 118 *Pterosperma ovum*. Reid (1974) synonymised Wall and Dale’s *Hystrichosphaera* n. sp.
10
11 119 with his *Spiniferites elongatus* but considered *Pterosperma ovum* to be synonymous with
12
13 120 his new species *Spiniferites belerius*, rather than *Spiniferites elongatus*, in having
14
15 121 processes of the same length covering the central body, an ovoid rather than elongate
16
17 122 central body, and in being smaller than *Spiniferites elongatus*. Given the range of
18
19 123 morphological variability now known for *Spiniferites elongatus* (e.g. central body length
20
21 124 of 40–59 μm in Reid 1974; 35–62 μm in Ellegaard et al. 2003; 42–64 μm in Van
22
23 125 Nieuwenhove et al. 2018), we accept that *Pterosperma ovum* and *Spiniferites elongatus*
24
25 126 are equivalent.

26
27
28
29
30
31 127 We make the following observations. Firstly, *Spiniferites elongatus* has a reported
32
33 128 central body length of 35–64 μm , compared with Gaarder’s two specimens with central
34
35 129 body lengths of 38 μm (her fig. 19a) and 46 μm (her fig. 19b). The smaller of her two
36
37 130 specimens might have been oriented at an oblique angle, but the larger one shows an
38
39 131 equatorial view and is well within the size range for *Spiniferites elongatus*. Secondly, the
40
41 132 illustrated specimens of *Pterosperma ovum* (Figure 1), and particularly the larger of the
42
43 133 two (her fig. 19b; Figure 1b), show shorter processes at the cingulum than at the poles.
44
45 134 Thirdly, the ratio of length vs. equatorial diameter for Gaarder’s illustrated specimens
46
47 135 (that for fig. 19a is 1.45 and that for fig. 19b is 1.37) falls within the range of variation
48
49 136 given for *Spiniferites elongatus* sensu lato by Van Nieuwenhove et al. (2018, table 1).
50
51
52
53
54
55
56
57
58
59
60

1
2
3 137 Fourthly, both *Pterosperma ovum* and *Spiniferites elongatus* have elevated abundances
4
5 138 off southern Ireland, as discussed above.

6
7
8 139 Ellegaard et al. (2003) incubated cysts of *Spiniferites elongatus* and discovered
9
10 140 that the emergent motile stage (Figure 2) had not been described previously. Rather than
11
12 141 erect a new species defined by the motile stage, they chose to transfer *Spiniferites*
13
14 142 *elongatus* to the motile-defined genus *Gonyaulax*, as *Gonyaulax elongata*. In doing so,
15
16 143 they emended *Gonyaulax elongata* to include details of the motile stage along with the
17
18 144 existing attributes of the cyst. Unified dinoflagellate nomenclature is permitted under the
19
20 145 Code, although contrary to their claims, Ellegaard et al. (2003) were not obliged to
21
22 146 follow this approach because the names of fossil taxa at the rank of genus and below do
23
24 147 not complete for priority with names of non-fossil taxa unless they are explicitly
25
26 148 considered as synonyms (Head et al. 2016; ICN Art. 11.7, 11.8). As with any name based
27
28 149 on a non-fossil, *Gonyaulax elongata* applies to all parts of the life cycle, and its cyst
29
30 150 would be referred to as the cyst of *Gonyaulax elongata*.

31
32
33
34
35 151

36 37 152 **2.1 Nomenclatural status of *Pterosperma ovum* Gaarder 1954**

38
39
40 153

41
42 154 Gaarder (1954) made clear that she was using botanical nomenclature because all the
43
44 155 family names she cited have botanical suffixes, e.g. Pterospermataceae. Gaarder
45
46 156 provided both a description for her new species and two illustrations (fig. 19a, b; Figure
47
48 157 1), each a line drawing of a separate specimen. Both specimens are from the same
49
50 158 location, Station 3 south of Ireland, where this species was found to be very common in
51
52 159 all samples. It is not known whether these two individuals are from the same sample and
53
54
55
56
57
58
59
60

1
2
3 160 represent a single gathering (and hence may constitute a single specimen; ICN Art. 8.2
4
5 161 and footnote), as several samples were collected from Station 3 (Gaarder 1954, p. 16).
6
7
8 162 However, we accept that both specimens represent the same species.
9

10 163 Although Gaarder's specimens are clearly cysts, and today might be curated and
11
12 164 used as type specimens, the illustrations themselves were presumably intended to serve
13
14 165 as the holotype, as was, and is, customary for unicellular non-fossil algal plankton that
15
16 166 are difficult to preserve (ICN Art. 8.1). Because two illustrations of separate individuals
17
18 167 are represented in her fig. 19 and may not be from a single gathering, we assume that the
19
20 168 holotype was not indicated. However, prior to 1 January, 1958, the holotype did not need
21
22 169 to be indicated under the ICN (Art. 40.1).
23
24
25

26 170 Gaarder's description was given exclusively in English. Although she provided
27
28 171 neither a Latin description nor diagnosis, this was not necessary prior to 1 January 1958
29
30 172 (ICN Art. 44.1). The specific epithet of *Pterosperma ovum* coincides with a Latin
31
32 173 technical term used in morphology at the time of publication. This condition is
33
34 174 acceptable for a specific epithet even though it would invalidate a generic name (ICN
35
36 175 Art. 20.2).
37
38
39

40 176 Accordingly, we accept that *Pterosperma ovum* is a name fulfilling all
41
42 177 requirements for valid publication at the time it was published.
43
44
45 178

46 47 179 **2.2 *Pterosperma ovatum* Pouchet 1894**

48

49 180
50
51 181 In 1894, M. Pouchet published two new species of his new genus *Pterosperma* collected
52
53 182 from the plankton off Svalbard and Jan Mayen: these were *Pterosperma rotundum* and
54
55
56
57
58
59
60

1
2
3 183 *Pterosperma ovatum* (Pouchet 1894, fig. 18a and fig. 18b respectively; reproduced here
4
5 184 as Fig. 3). *Pterosperma ovatum* has a markedly elongate central body, granular cell
6
7
8 185 contents, and membranous septa that are notably higher at the poles than the equator. No
9
10 186 discrete processes or branching of process terminations are evident from either Pouchet's
11
12 187 brief description or his simple line figure. Nonetheless, allowing for the standards of
13
14 188 documentation at that time, the single illustrated specimen bears at least a superficial
15
16
17 189 resemblance to *Spiniferites elongatus* and was collected from a region where this species
18
19 190 is known to be present (de Vernal et al. 2020).

20
21 191 Lemmermann (1903) transferred *Pterosperma ovatum* to the oocystacean
22
23 192 (chlorophyte) genus *Trochiscia* Kützing 1834 as *Trochiscia ovata* (Pouchet 1894)
24
25
26 193 Lemmermann (1903). Parke et al. (1978) selected Pouchet's illustration of *Pterosperma*
27
28 194 *rotondum* as the type for the genus *Pterosperma* (which Pouchet had not been obliged to
29
30 195 do at the time he proposed the genus), but they considered *Pterosperma ovatum* to
31
32 196 "represent either a *Pterosperma* under coverslip pressure ... or a dinophycean cyst"
33
34
35 197 (Parke et al. 1978, p. 241).

36
37 198 As with *Pterosperma ovum* Gaarder 1954, we accept that *Trochiscia ovata* is a
38
39 199 non-fossil name fulfilling all requirements for valid publication. While we acknowledge
40
41 200 that *Trochiscia ovata* may also be equivalent to *Spiniferites elongatus*, and would have
42
43 201 priority over *Pterosperma ovum*, the probability of this being the case is much less than
44
45 202 for *Pterosperma ovum*. Given the uncertainty as to what Pouchet was actually recording,
46
47 203 including its size, we recommend that the name *Trochiscia ovata* be restricted to the
48
49 204 illustration by Pouchet (1894, fig. 18a). Should this recommendation not be followed, we
50
51 205 note that *Trochiscia ovata* cannot be transferred to the genus *Gonyaulax* under its current
52
53
54
55
56
57
58
59
60

1
2
3 206 name because the epithet is already occupied by *Gonyaulax ovata* Matzenauer 1933; a
4
5 207 new name would be required, which would then be a junior homotypic synonym of
6
7
8 208 *Pterosperma ovum* (ICN Art. 11.4).
9

10 209

11 12 210 **2.3 *Gonyaulax ovum* and *Spiniferites elongatus* under dual nomenclature**

13
14
15 211

16
17 212 While there are advantages in a unified nomenclature, the name *Gonyaulax elongata*
18
19 213 fails to maintain the connection with the important fossil-defined genus *Spiniferites*
20
21 214 (Ellegaard et al. 2018). However, simply rejecting this name in favour of *Spiniferites*
22
23 215 *elongatus* leaves no name available for the motile stage in the life cycle.

24
25
26 216 *Pterosperma ovum* presents a solution. This species corresponds to *Spiniferites*
27
28 217 *elongatus* but is a non-fossil species, having been described from the plankton. By
29
30 218 transferring *Pterosperma ovum* to the genus *Gonyaulax*, as *Gonyaulax ovum*, and
31
32 219 emending this species to provide both cyst and motile stage characters, as we have done
33
34 220 below (Systematics section), a name is created that fulfills the role of *Gonyaulax*
35
36 221 *elongata* while liberating the name *Spiniferites elongatus* for its application exclusively
37
38 222 with cysts. A dual nomenclature is thereby created for this overlap of species concepts.

39
40
41
42 223 *Gonyaulax elongata* and *Gonyaulax ovum* do not compete for priority because
43
44 224 *Gonyaulax elongata* remains a fossil-species (its type is that of *Spiniferites elongatus*)
45
46 225 despite having been transferred to *Gonyaulax*. As a non-fossil, *Gonyaulax ovum*
47
48 226 appropriately belongs in the non-fossil genus *Gonyaulax* even though its type is a cyst.
49
50 227 The name *Gonyaulax elongata* has not been widely adopted, and its loss will not threaten
51
52 228 nomenclatural stability.
53
54
55
56
57
58
59
60

1
2
3 229 Accordingly, we accept that *Pterosperma ovum* is the non-fossil equivalent of the
4
5 230 fossil defined *Spiniferites elongatus* and, based on the discovery that cysts assignable to
6
7 231 *Spiniferites elongatus* produce a motile cell referable to the genus *Gonyaulax* (Ellegaard
8
9 232 et al. 2003), we propose the new combination *Gonyaulax ovum* (Systematics section).
10
11 233 This name refers to all stages of the life cycle, whereas *Spiniferites elongatus* applies
12
13 234 only to cysts, whether fossil or modern.
14
15
16
17 235
18
19 236
20
21
22 237 **3. *Gonyaulax lewisiae* n. sp. and *Spiniferites membranaceus* Reid 1974**
23
24 238
25

26 239 *Spiniferites membranaceus* (Rossignol 1964) Sarjeant 1970 has a distinctive antapical
27
28 240 granular flange connecting the two slender dorso-antapical processes (Van Nieuwenhove
29
30 241 et al. 2020; Plate 2). It was initially recorded by Rossignol (1964, as *Hystrichosphaera*
31
32 242 *furcata* var. *membranacea*) from Pleistocene or Holocene deposits of the Ashkelon
33
34 243 borehole St. 39D, coastal plain, Israel, and has since been recorded frequently in modern
35
36 244 and other Quaternary sediments (de Vernal et al. 2020).
37
38
39

40 245 Lewis et al. (1999) isolated live cysts of *Spiniferites membranaceus* from surface
41
42 246 sediment off southwest England and from the southwest North Sea, and obtained cultures
43
44 247 from them revealing in detail the equivalent motile stage. The motile stage (Fig. 4),
45
46 248 although distinctive, was not formally described, but was recognised as belonging to the
47
48 249 genus *Gonyaulax* and referred to the *Spinifera* group of Kofoid (1911).
49
50

51 250 Ellegaard et al. (2003) isolated a single live cyst of *Spiniferites membranaceus*
52
53 251 from surface sediment collected near Drogheda, Ireland, which germinated to give a
54
55
56
57
58
59
60

1
2
3 252 culture used to document the motile stage. The culture then produced cysts. This strain
4
5 253 (UW398) was also subjected to molecular phylogenetic analysis. Based on this strain,
6
7
8 254 Ellegaard et al. (2003) expanded the description already provided by Lewis et al. (1999)
9
10 255 for both the motile stage and the cyst. Incorporating data from Lewis et al. (1999),
11
12 256 Ellegaard et al. (2003) noted considerable intraspecific variation when comparing both
13
14 257 cyst and motile stage morphologies, even though molecular phylogenetic analysis
15
16
17 258 indicated conspecificity. The motile stage nonetheless unquestionably belonged to the
18
19 259 genus *Gonyaulax*. Rather than propose a new species typified by the motile stage,
20
21 260 Ellegaard et al. (2003) chose to transfer *Spiniferites membranaceus* to the genus
22
23 261 *Gonyaulax*, as *Gonyaulax membranaceus*, thus uniting both thecal and cyst-based
24
25
26 262 characters under a single species name. While they were at liberty to make this
27
28 263 nomenclatural change under the ICN, and there are certainly benefits to this approach,
29
30 264 several problems were created. Removing the link to *Spiniferites* obscured the
31
32 265 connection of this cyst morphotype to potentially related species within the fossil record.
33
34
35 266 In addition, if their combination were accepted and used, the action would result in the
36
37 267 loss of a name frequently recorded in the Quaternary literature.

38
39
40 268 Our solution is to retain the name *Spiniferites membranaceus* for fossil cysts
41
42 269 while establishing *Gonyaulax lewisiae* n. sp. as a new name typified by the motile cell
43
44 270 (Systematics section). *Spiniferites membranaceus* (Rossignol 1964) Sarjeant 1970 is
45
46 271 therefore considered equivalent to *Gonyaulax lewisiae* n. sp. using dual nomenclature.

47
48
49 272

50
51 273

52
53
54 274 **4. Systematics**

1
2
3 275
4

5 276 Modified Kofoidian plate labelling is used in which homologous plates are indicated by
6
7
8 277 an asterisk following Bujak (1980) and Fensome et al. (1993, text fig. 62). Sulcal plate
9
10 278 labelling follows Evitt (1985). We follow the recommendations of Gravendyck et al.
11
12 279 (2021) for the synonymies, using the equality symbol (=) for homotypic (nomenclatural)
13
14 280 synonyms and an identity symbol (\equiv) for heterotypic (taxonomic) synonyms.
15
16

17 281
18

19 282 Division DINOFLAGELLATA (Bütschli 1885) Fensome et al. 1993 emend. Adl et al.

20
21 283
22
23

2005

24 284

Subdivision DINOKARYOTA Fensome et al. 1993

25
26 285

Class DINOPHYCEAE Pascher 1914

27
28 286

Order GONYAULACALES Taylor 1980

29
30 287

Suborder GONYAULACINEAE (Autonym)

31
32 288

Family GONYAULACACEAE Lindemann 1928

33
34 289

Subfamily GONYAULACOIDEAE (Autonym)

35
36 290

Genus *Gonyaulax* Diesing 1866 emend. Dodge 1989

37
38
39
40 291
41

42 292 **Type.** The holotype of the non-fossil species *Gonyaulax spinifera* (Claparède and

43
44 293

Lachmann) Diesing 1866

45
46
47 294
48

49 295

Nomenclatural status. A non-fossil genus.

50
51 296
52

53
54 297

Comments. Dodge (1989) restricted the genus *Gonyaulax* to species having the

1
2
3 298 tabulation Po, 3', 2a, 6'', 6c, 4–8s, 5''', 1p, 1''''', and included in his redescription the
4
5 299 observation that many species form thick-walled cysts. His redescriptions of the species
6
7 300 he assigned to this genus included information about the resting cysts where available.
8
9 301 As noted above, at least seven fossil-genera, are attributable to *Gonyaulax spinifera* and
10
11 302 its allies (Head 1996; Head et al. submitted). Of the 71 non-fossil species that belong to
12
13 303 the genus *Gonyaulax* (Gómez 2012), only 21 can be assigned to this genus using
14
15 304 Dodge's 1989 generic concept, these being 17 species listed by Dodge, plus four
16
17 305 additional ones (Mertens and Carbonell-Moore 2018). Much additional research is
18
19 306 therefore needed to check and, if necessary, reattribute these species. Meanwhile, we
20
21 307 accept Dodge's emended concept of *Gonyaulax*.
22
23
24
25

26 308

27 309

28 310 *Gonyaulax ovum* (Gaarder 1954) n. comb., emend.
29
30

31 311 Figures 1, 2
32
33

34 312
35
36

37 313 **Basionym.** *Pterosperma ovum* Gaarder 1954, p. 16, fig. 19a, b.
38
39

40 314

41 315 **Previous record.**

42 316 2003 *Gonyaulax elongata* Ellegaard et al., p. 154–156, figs. 1–30.
43
44

45 317

46 318 **Equivalent fossil-species.** *Spiniferites elongatus* Reid 1974 (Ellegaard et al. 2003).
47
48

49 319
50
51
52
53
54
55
56
57
58
59
60

1
2
3 320 **Holotype.** Gaarder 1954, fig. 19b (designated here). Illustration of cyst collected from
4
5 321 the plankton.
6

7
8 322

9
10 323 **Type locality.** Station 3, south of Ireland, 49° 32' N; 10° 49' W (Gaarder 1954).
11

12 324

13
14 325 **Etymology.** Latin *ovum*, egg; presumably with reference to the elongate shape of the
15
16 326 central body. Noun in apposition.
17

18
19 327

20
21 328 **Diagnosis.** Motile cell with conical epitheca featuring slight shoulders and short apical
22
23 329 horn, and conical hypotheca with flat antapex. Often pronounced reticulated plates; few
24
25 330 pores, occurring mostly on cingular margins. Plate 6'' is an elongated triangle; cingular
26
27 331 displacement of 2–3 cingular widths; overhang up to 2.5 cingular widths. An antapical,
28
29 332 triangular flange and 0–8 antapical spines can be present. Elongate resting cyst with
30
31 333 finely granulate outer wall and exclusively gonal processes. Based on Ellegaard et al.
32
33 334 (2003, p. 161, 163, table 4).
34
35 335

36
37 336 **Description of motile stage.** Conical epitheca with slight shoulders and short apical
38
39 337 horn; hypotheca conical with flat antapex. Cell brown, nearly circular in polar view;
40
41 338 often diamond-shaped in ventral or dorsal view owing to triangular antapical flange.
42
43 339

44
45 340 Tabulation S-type typical for genus (see Ellegaard et al. 2003, figs. 1–3),
46
47 341 tabulation formula 3', 2a, 6'', 6c, ?s, ps, 1p, 6'''*, 1'''''. Plates show variable but often
48
49
50
51
52
53
54
55
56
57
58
59
60 pronounced reticulation that may occur also on cingulum, sulcus and flanges; newly

1
2
3 342 divided cells lack ornamentation. Plates and plate boundaries often difficult to discern;
4
5 343 plates have few pores, occurring mostly on cingular margins.
6

7
8 344 Third apical plate (3') small, often difficult to distinguish from first anterior
9
10 345 intercalary (1a). On most specimens, second anterior intercalary (2a) is difficult to
11
12 346 separate from plates 1' and 3'. Ventral pore clear only on some specimens. Apical pore
13
14 347 complex (APC) surrounded by smooth ridge formed by edges of surrounding plates.
15
16 348 Plates 2' and 1a meet mid-dorsally. Third precingular plate (3'') broad, overlaps all
17
18 349 adjoining plates (keystone plate). Plate 6'' is an elongated triangle.
19

20
21 350 Cingulum wide and deep, ends of cingulum form an angle of 16–33° with main
22
23 351 axis of cell; displacement of 2–3 cingular widths; overhang up to 2.5 cingular widths.
24
25 352 Flanges (lists) present on cingular margins.
26

27
28 353 Sulcus deep, widens broadly towards antapex, sulcal depression ending near
29
30 354 upper cingular margin. Anterior part of sulcus narrow, with hook-shaped anterior sulcal
31
32 355 plate (as). Boundaries of sulcal plates obscured at anterior end, clear in antapical part of
33
34 356 sulcus. Posterior sulcal plate (ps) broad, relatively short. Boundary between left (ls) and
35
36 357 right (rs) sulcal plates originates from middle of anterior boundary of ps plate. First
37
38 358 postcingular homolog (1''*) is rectangular and small and lies within the sulcus; 2''* is an
39
40 359 elongated triangle. Anterior intercalary plate (1p) barely touches antapical plate (1''').
41

42
43 360 Flanges present on plates 1s, 6''* and 1''''; 0–8 small spines on plate 1'''''. All
44
45 361 flanges and spines variably developed, sometimes absent. Triangular flange on plate 1'''''
46
47 362 characteristic but often small, not always visible under light microscopy.
48

49
50 363 Plate overlap pattern as described for *G. digitalis* (Lewis et al. 2001). Based on
51
52 364 Ellegaard et al. (2003, p. 154, 156).
53
54
55
56
57
58
59
60

365

366 **Description of cyst.** Central body rounded, elongate in lateral view; circular in polar
367 view; no apical protuberance. Outer wall layer of central body thin, finely granulate;
368 inner wall layer smooth, about 0.3 µm thick. Low sutural ridges with a width of ~0.3 µm
369 occur on the cyst surface and reveal fine details of tabulation. They are faintly visible
370 under light microscopy and best seen under SEM (pls. 7–10 in Van Nieuwenhove et al.
371 2020). Processes gonal, variable in length, from an average of 2 to 8 µm (n = 5, 4–8
372 processes measured per cyst). Antapical processes typically the longest (6–12 µm, n =
373 11), cingular processes are shortest (0–7 µm, n = 11), except for cysts with reduced
374 processes, where all are approximately equal in length. Fully developed processes are
375 distally trifurcate with bifid terminations; reduced processes may taper to a point, end
376 bluntly, or end with slight fork. Septa follow sutures, vary from low to high, usually rise
377 towards processes, and best developed at antapex, but may cover entire central body.
378 Cavation may occur under processes especially at apex, extreme at antapex along the
379 1p/1''', 3'''*/1'''' and 5'''*/1'''' sutures. Extension of septa onto intraplate areas often
380 makes the latter appear rounded.

381 SEM studies record the APC and ventral pore, as well as the apical plate series
382 and two anterior intercalary plates (1a, 2a) which are as for the motile cell, except that
383 the small 3' plate while assumed present is not clearly observed (pls. 7 in Van
384 Nieuwenhove et al. 2020). The sulcal tabulation can be clearly expressed under SEM
385 with the anterior, right accessory, right, left, and posterior sulcal plates (as, ras, rs, ls, ps)
386 and their boundaries being observed. Plate 1'''* is small and narrow and inside the sulcus

1
2
3 387 which is represented by a shallow depression in the cyst (pl. 8 in Van Nieuwenhove et al.
4
5 388 2020). Cingulum displaced by about two cingular widths, with no overlap.
6

7
8 389 Tabulation formula APC, 3', 2a, 6'', 6c, s, 1p, 6'''*, 1'''''. Archeopyle formed by
9
10 390 loss of third precingular plate (3''). Based on Gaarder (1954, fig. 19a, b), Ellegaard et al.
11
12 391 (2003, p. 156, figs. 20–26), Van Nieuwenhove et al. (2018).
13

14
15 392

16
17 393 **Dimensions of motile cell.** Length 32–41 μm , width 28–34 μm , 25 specimens measured;
18
19 394 cingular width 2.5–3.5 μm (Ellegaard et al. 2003).
20

21
22 395

23
24 396 **Dimensions of cyst.** Holotype length 46 μm (Gaarder 1954, fig. 19b); range: length 35–
25
26 397 62 μm , width 20–32 μm , 19 specimens measured (Ellegaard et al. 2003).
27

28
29 398

30
31 399 **Gene sequences.** NCBI GenBank accession number is AY154964 for strain UW388
32
33 400 (table 3 in Ellegaard et al. 2003). Individual cysts from the Beaufort Sea identified as
34
35 401 *Spiniferites elongatus s.l.* cyst 1, 2, 6, 8, and 9 have the following accession numbers:
36
37 402 KU358942, KU358943, KU358947, KU358949, and KU358950 (fig. 7 in Van
38
39 403 Nieuwenhove et al. 2018).
40
41

42
43 404

44
45 405 **Modern distribution.** The motile stage is presently known only from the germination of
46
47 406 cysts collected from Nova Scotia, Orkney, and the English North Sea coast (Ellegaard et
48
49 407 al. 2003). The cyst, under the name *Spiniferites elongatus*, is a common species of polar
50
51 408 and subpolar environments (de Vernal et al. 2020).
52

53
54 409
55
56
57
58
59
60

1
2
3 410
4

5 411

Gonyaulax lewisiae n. sp.

7
8 412

Figure 4

9
10 413
11

12 414 **Previous records.**

13
14 415 1999 *Spiniferites membranaceus* (Rossignol 1964) Sarjeant 1970; Lewis et al., p. 115–

15
16 416 117, figs. 1–20.
17
18

19 417
20

21 418 2003 *Gonyaulax membranacea* (Rossignol 1964) Ellegaard et al., p. 157, 163, figs. 31–

22
23 419 45, 47, 51.
24
25

26 420
27

28 421 **Equivalent fossil-species.** *Spiniferites membranaceus* (Rossignol 1964) Sarjeant 1970

29
30 422 (Lewis et al. 1999; Ellegaard et al. 2003; Mertens et al. 2018).
31
32

33 423
34

35 424 **Holotype.** Lewis et al. 1999, fig. 18. Illustration of motile cell grown from culture

36
37 425 originating from a single wild cyst identified as *Spiniferites membranaceus*.
38
39

40 426
41

42 427 **Type locality.** Offshore UK (Cornwall and southwest North Sea, unspecified; Lewis et

43
44 428 al. 1999).
45
46

47 429
48

49 430 **Etymology.** Named for British biologist Jane Lewis.
50
51

52 431
53

54 432 **Diagnosis.** Motile cell prolate, ovoidal, slightly longer than wide, with little dorsoventral
55
56
57
58
59
60

1
2
3 433 flattening; apical horn inconspicuous, shoulders weakly angular. Plates usually well
4
5 434 formed with smooth margins, reticulate, except in sutural area where there is reduced or
6
7
8 435 no reticulation. Cingulum displaced by 2.5–4.0 cingular widths, overhang of 2–4 widths.
9
10 436 6'' approximately triangular. Posterior sulcal plate narrow. Between two and four
11
12 437 antapical spines where one is more prominent, may be finned. Resting cyst with a
13
14 438 broadly ovoid central body; outer surface microgranulate to microrugulate. Processes
15
16 439 exclusively gonal. Sutural septa mostly low except at antapex. Cingulum inclined, offset
17
18 440 by one or two times its width. Based on Ellegaard et al. (2003, p. 157, 158, table 4).
19
20
21
22
23

24 441

24 442 **Description of motile stage.** Cell prolate, ovoidal, slightly longer than wide, with little
25
26 443 dorsoventral flattening; apical horn inconspicuous, shoulders weakly angular. Plates well
27
28 444 formed, strongly reticulate, except in sutural area where there is reduced or no
29
30 445 reticulation. Cingular plates reticulate, with pronounced rows of pores on margins; ridges
31
32 446 perpendicular to cingulum extend between pores on opposite margins.
33
34

35 447 Tabulation S-type gonyaulacacean: APC, 3', 2a, 6'', 6c, s, 6''', 1p, 1'''. Apical
36
37 448 pore complex (APC) smooth, sometimes with low central ridge, its margin marked by
38
39 449 low ridge surrounded by low flange created by apical plates. First apical plate (1') narrow
40
41 450 bearing single row of pores; second apical plate (2') large, curves around dorsal surface
42
43 451 of apical horn to contact the first apical intercalary (1a); and third apical plate (3') small
44
45 452 and narrow and may be difficult to discern but usually separable by dissection or visible
46
47 453 under SEM. Plate 1a large, adjoins 3' and second anterior intercalary (2a), the latter
48
49 454 extending alongside 1' and marked at adapical boundary by ventral pore.
50
51
52
53
54
55
56
57
58
59
60

1
2
3 455 Six precingular plates, 2'' being widest, 6'' approximately triangular.

4
5 456 Cingulum has six plates, is excavated, overhangs by 2 to 4 cingular widths, angle
6
7
8 457 of cingulum (angle made by intersection of line joining ends of cingulum with long axis
9
10 458 of cell) 20–29°, has a displacement of 2.5 to 4.0 cingular widths.

11
12 459 Sulcus excavated, extends to antapex, bears narrow sulcal lists; total number of
13
14 460 sulcal plates not fully determined owing to overlap and overhang of cingulum, but at
15
16
17 461 least five based on dissection of region. Posterior sulcal plate smooth with single row of
18
19 462 large pores around lateral and anterior margins. Anterior sulcal plate (as) elongate,
20
21 463 extends onto epitheca. Anterior sulcal region slightly widened.

22
23
24 464 Six postcingular homologs of which 1'''* is narrow, may be ridged, consistently
25
26 465 has single row of pores. Posterior intercalary plate (ps) lies below 1'''*, next to sulcus.
27
28 466 Single antapical plate (1'''''); antapical spines variably developed along suture between
29
30 467 1'''* and ps. Cells may have two spines, or three to four small spines, one spine often
31
32 468 more prominent than the others; spines may be narrowly conical or may bear fins. Based
33
34
35 469 on Lewis et al. (1999; Fig. 4).

36
37
38 470

39
40 471 **Description of cyst.** Spiniferate, the central body rounded to broadly ovoid with a <1.0
41
42 472 µm two-layered wall, the inner layer thicker than the outer. No apical protuberance.
43
44 473 Outer surface of cyst microgranulate to microrugulate. Tabulation S-type sexiform
45
46 474 gonyalacoid with the formula APC, 4', 6'', 6c, s, ps, 1p, 6'''*, 1''''', as indicated by sutural
47
48 475 septa and exclusively gonal processes; details of the apical plates and their contact (or
49
50 476 not) with the APC are not recorded. Sutural septa are often perforate, have smooth distal
51
52
53 477 crests, and are variable in height although mostly low except at the antapex. The

1
2
3 478 archeopyle is formed by loss of the third precingular plate (3''), operculum free.
4
5 479 Archeopyle slightly reduced with well defined angles. Cingulum inclined and offset by
6
7 480 one or two times its width; delineated by crests and gonol processes on both anterior and
8
9 481 posterior margins. Sulcus moderately wide. Sulcal tabulation suppressed, usually only the
10
11 482 posterior plate (ps) well expressed. A prominent suturocavate extension marking the
12
13 483 boundary between plates 4''* and 1'' is characteristic. This extension is effectively two
14
15 484 antapical processes joined by an equally high septum along the 4''*/1'' boundary. Other
16
17 485 processes are usually solid with trifurcate tips bearing Y-shaped to recurved bifurcate
18
19 486 terminations. Proximal ends of processes may be perforate or fenestrate, with all
20
21 487 processes on a single cyst being of approximately similar length. Reduced septa and
22
23 488 processes may occur. Based on Lewis et al. (1999), Ellegaard et al. (2003), Mertens et al.
24
25 489 (2018), Van Nieuwenhove et al. (2020).

30
31 490

32
33 491 **Intraspecific variability.** Lewis et al. (1999) reported considerable variation in process
34
35 492 length and variability for cysts produced in culture, with some cysts lacking processes
36
37 493 and others almost devoid of tabulation. Some of these variations were observed in wild
38
39 494 cysts obtained from sediments off Cornwall.

40
41
42 495 From a cyst identified morphologically as *Spiniferites membranaceus* collected
43
44 496 from surface sediment near Drogheda, Ireland, Ellegaard et al. (2003) established a
45
46 497 culture (strain UW398) that formed cysts. Despite normal initial cyst morphology and
47
48 498 genetic sequences, the resulting motile cells and cysts were found to differ significantly
49
50 499 in morphology from what is now the type material described by Lewis et al. (1999).

1
2
3 500 For the motile cells, the thecal plates were difficult to discern and had a reduced
4
5 501 reticulate ornament comprising circular depressions, each surrounded by a rim and in
6
7 502 some cases with a pore at the centre. The cells usually had two spines on the posterior
8
9 503 sulcal rim, 2–4 μm long, with one often more prominent. The suppression of a reticulate
10
11 504 ornamentation and the prominent circular depressions were found to be the
12
13 505 distinguishing characters of this strain, although Ellegaard et al. (2003) noted a tendency
14
15 506 towards similarly reduced reticulation in the type material (strain UW345) studied by
16
17 507 Lewis et al. (1999).

18
19 508 The cysts produced in culture did not have well developed processes or
20
21 509 significant expression of tabulation, and specimens illustrated by Ellegaard et al. (2003,
22
23 510 figs. 33–36) would not be assignable to the genus *Spiniferites*.

24
25 511 Ellegaard et al. (2003) considered the substantial morphological divergence of
26
27 512 strain UW345 to be an example of strong intraspecific variation for this species. While
28
29 513 this undoubtedly the case (see also Lewis et al. 1999), more research would be helpful to
30
31 514 establish the effects of laboratory culturing on the morphological development of both
32
33 515 cyst and motile stage.

34
35 516

36
37 517 **Dimensions of motile cell.** Holotype: width 35 μm (measured from Lewis et al. 1999,
38
39 518 fig. 18). Range: length 30–48 μm , width 23–40 μm , 40 specimens measured (Lewis et al.
40
41 519 1999); length 31–37 μm , width 25–30 μm , 40 specimens measured (Ellegaard et al.
42
43 520 2003).

44
45 521

1
2
3 522 **Dimensions of cyst.** Length 41–54 μm , width 37–50 μm , 24 specimens measured (Lewis
4
5 523 et al. 1999); diameter 28–35 μm , 10 specimens measured (Ellegaard et al. 2003).
6
7

8 524
9

10 525 **Gene sequences.** NCBI GenBank accession numbers are as follows: AY154961 for strain
11
12 526 UW413 (and UW414), AY154965 for strain UW398 (table 3 in Ellegaard et al. 2003).
13
14

15 527
16

17 528 **Remarks.** The holotype here designated (Lewis et al. 1999, fig. 18) is an illustration of
18
19 529 one of numerous motile cells reared from laboratory culturing of individual cysts. These
20
21 530 cysts were collected from surface sediments of Cornwall and southwest North Sea. It is
22
23 531 not known whether the illustrated specimens (Lewis et al. 1999, figs. 13–19) are from the
24
25 532 same culture or several cultures raised from different cysts. Accordingly, a single
26
27 533 illustration is selected as the holotype.
28
29

30
31 534 The intraspecific variability for both the motile stage and cyst is described by
32
33 535 Lewis et al. (1999) and Ellegaard et al. (2003). *Spiniferites membranaceus* is discussed
34
35 536 by Mertens et al. (2018), Gurdebeke et al. (2018), and Van Nieuwenhove et al. (2020).
36
37

38 537
39

40 538 **Modern distribution.** The motile stage is presently known only from the germination of
41
42 539 cysts collected off southwestern England and southwestern North Sea (Lewis et al. 1999)
43
44 540 and from near Drogheda, Ireland (Ellegaard et al. 2003). The cyst, under the name
45
46 541 *Spiniferites membranaceus*, is a common Quaternary species distributed mostly in low to
47
48 542 middle latitudes (de Vernal et al. 2020).
49
50

51 543
52
53

54 544
55
56
57
58
59
60

1
2
3 545 Genus *Spiniferites* Mantell 1850, emend. Sarjeant 1970
4

5 546
6

7
8 547 **Type.** The lectotype of the fossil species *Spiniferites ramosus* (Ehrenberg 1837) Mantell
9

10 548 1854. Holotype not designated by Ehrenberg. Lectotype designated by Davey and
11

12 549 Williams (1966) as Ehrenberg, 1837, pl. 1, fig. 15. Upper Cretaceous.
13

14 550
15

16
17 551 **Nomenclatural status.** A fossil-genus.
18

19 552
20

21 553 **Comments.** A large genus presently containing at least 112 species (Fensome et al.
22

23 554 2019) of which only ~16 are presently considered extant.
24

25 555
26

27 556
28

29 557 *Spiniferites elongatus* Reid 1974, emend. Van Nieuwenhove et al. 2018
30

31 558 Plate 1
32

33 559
34

35 560 **Basionym.** *Spiniferites elongatus* Reid 1974 in *Nova Hedwigia* 25, 602–603, pl. 3, figs.
36

37 561 23–24; emend. Van Nieuwenhove et al. 2018 in *Palynology*: 42(S1), 126–128.
38

39 562
40

41 563 **Synonymy.**
42

43 564 = *Spiniferites ellipsoideus* Matsuoka 1983 in *Palaeontographica*, Abteilung B 187: 132–
44

45 565 133, pl. 13, figs. 6a–b, 7a–b; according to Gurdebeke et al. (2018, p. 98), Mertens et
46

47 566 al. (2018, p. 21), and Van Nieuwenhove et al. (2018, p. 126).
48
49
50
51
52
53
54
55
56
57
58
59
60

1
2
3 567 = *Spiniferites frigidus* Harland and Reid in Harland et al. 1980 in Grana 19: 213–216,
4
5 568 figs. 2A–J, text-fig. 3; according to Mertens et al. (2018, p. 21) and Van Nieuwenhove
6
7 569 et al. (2018, p. 126, 132).

8
9
10 570 = *Rottnestia amphicavata* Dobell and Norris in Harland et al. 1980 in Grana 19: 218–220,
11
12 571 text-figs. 4A–N, 5–7; according to Mertens et al. (2018, p. 21) and Van Nieuwenhove
13
14 572 et al. (2018, p. 126, 132).

15
16
17 573

18
19 574 **Equivalent non-fossil species.** *Gonyaulax ovum* (Gaarder 1954) n. comb., emend.

20
21
22 575

23
24 576 **Holotype.** Reid (1974, p. 602–603, pl. 3, figs. 23–24). From modern sediment.

25
26
27 577

28
29 578 **Type locality.** Estuary of the River Ythan, northeastern Scotland (Reid 1974).

30
31
32 579

33
34
35 580

36
37 581 *Spiniferites elongatus* Reid 1974, emend. Van Nieuwenhove et al. 2018, forma *frigidus*
38
39 582 (Harland and Reid in Harland et al. 1980) n. stat.

40
41
42 583

43
44 584 **Basionym.** *Spiniferites frigidus* Harland and Reid in Harland et al. 1980 in Grana 19:
45
46 585 213–216, figs. 2A–J, text-fig. 3.

47
48
49 586

50
51
52 587 **Synonymy.**

1
2
3 588 ≡ *Rottnestia amphicavata* Dobell and Norris in Harland et al. 1980 in Grana 19: 218–220,
4
5 589 text-figs. 4A–N, 5–7; according to Mertens et al. (2018, p. 21) and Van Nieuwenhove
6
7 590 et al. (2018, p. 126, 132).
8
9

10 591

11
12 592 **Holotype.** Harland et al. 1980, figs. 2G–J, text-fig. 3. From modern sediment.
13

14 593

15
16
17 594 **Type locality.** Southern Beaufort Sea, Mackenzie Delta offshore region of northern
18
19 595 Canada.
20

21 596

22
23 597 **Comments on nomenclature.** In synonymising *Spiniferites frigidus* (and *Rottnestia*
24
25 598 *amphicavata*) with *Spiniferites elongatus*, Van Nieuwenhove et al. (2018) noted that
26
27 599 *Spiniferites frigidus* represents an end member in which the hypocyst is exceptionally
28
29 600 suturocavate (Plate 1, fig. 9–12). These authors recommended that specimens assignable
30
31 601 to *Spiniferites frigidus* be referred to as the “Beaufort” morphotype of *Spiniferites*
32
33 602 *elongatus*. We here use a formal approach, and name it as *Spiniferites elongatus* forma
34
35 603 *frigidus* n. stat. to distinguish from other morphotypes including that represented by the
36
37 604 holotype, now *Spiniferites elongatus* forma *elongatus* (autonym).
38
39

40
41 605 Although genetic sequencing shows no significant differences between
42
43 606 morphotypes (Van Nieuwenhove et al. 2018), it is not presently known whether all
44
45 607 morphotypes now attributed to *Spiniferites elongatus* have the same stratigraphic ranges.
46
47 608 In the Bering Sea, *Spiniferites elongatus* forma *frigidus* has a lowest recorded occurrence
48
49 609 in the Upper Miocene (as *Spiniferites frigidus* in Matsuoka and Bujak 1988) whereas the
50
51 610 morphotype formerly assigned to *Spiniferites ellipsoideus* possibly ranges into the Lower
52
53
54
55
56
57
58
59
60

1
2
3 611 Miocene (Van Nieuwenhove et al. 2018 and references therein). This leaves open the
4
5 612 question of whether the earliest records of *Spiniferites elongatus* s.l. are genetically the
6
7 613 same as modern populations, which are characterised by a high degree of morphological
8
9 614 variability.

10
11
12 615

13
14
15 616

16
17 617 *Spiniferites membranaceus* (Rossignol 1974) Sarjeant 1970

18
19 618 Plate 2

20
21
22 619

23
24 620 **Basionym.** *Hystrichosphaera furcata* var. *membranacea* Rossignol 1974 in Revue de
25
26 621 micropaléontologie 7, 86, pl. 1, figs. 4, 9–10; pl. 3, figs. 7, 12.

27
28
29 622

30
31 623 **Synonymy.**

32
33 624 ≡ *Hystrichosphaera ramosa* var. *membranacea* (Rossignol 1964) Davey and Williams
34
35 625 1966b, p. 37.

36
37 626 ≡ *Hystrichosphaera membranacea* (Rossignol 1964) Wall 1967, p. 102.

38
39 627 ≡ *Spiniferites membranaceus* (Rossignol 1964) Sarjeant 1970, p. 76.

40
41
42 628

43
44 629 **Equivalent non-fossil species.** *Gonyaulax lewisiae* n. sp.

45
46
47 630

48
49 631 **Holotype.** Rossignol 1964, pl. 1, figs. 4, 9–10. Pleistocene or Holocene sediments
50
51 632 (Rossignol 1964).

52
53
54 633

1
2
3 634 **Type locality.** Ashkelon borehole St. 39D, coastal plain, Israel.
4
5

6 635
7

8 636
9

10 637 **5. Summary**
11

12 638
13

14 639 We have considered in detail the cyst-defined extant fossil-species *Spiniferites elongatus*
15
16 640 and *Spiniferites membranaceus*, reported frequently from late Cenozoic deposits, using a
17
18
19 641 dual nomenclatural approach.
20

21 642 Ellegaard et al. (2003) incubated cysts that they had assigned to *Spiniferites*
22
23 643 *elongatus* and discovered that the emergent motile stage had not been described
24
25 644 previously. They emended this species to incorporate features of the motile stage and
26
27 645 transferred it to the non-fossil genus *Gonyaulax*, as *Gonyaulax elongata*. Our approach
28
29 646 retains the name *Spiniferites elongatus* so that it may be applied exclusively to the cysts
30
31 647 and their fossil record, as originally intended. Meanwhile, the name *Pterosperma ovum*
32
33 648 refers to an organism now recognised as the cyst of *Spiniferites elongatus* but was
34
35 649 collected from the plankton and is clearly a non-fossil. We transfer the species
36
37 650 *Pterosperma ovum* to the genus *Gonyaulax*, as *Gonyaulax ovum*, and emend this species
38
39 651 to incorporate the description of Ellegaard et al. (2003) for the motile stage of their
40
41 652 *Gonyaulax elongata*. This provides an equivalent non-fossil name for *Spiniferites*
42
43 653 *elongatus* in accordance with the practice of dual nomenclature, even though both
44
45 654 species are typified by a cyst.
46
47
48
49
50

51 655 Van Nieuwenhove et al. (2018) broadened the circumscription of *Spiniferites*
52
53 656 *elongatus* to include a wide range of morphotypes including that initially described as
54
55
56
57
58
59
60

1
2
3 657 *Spiniferites frigidus* and which these authors named the “Beaufort morphotype”. We
4
5 658 propose the formal name *Spiniferites elongatus* forma *frigidus* n. stat. for this distinctive
6
7 659 morphotype with extreme suturocavation on the hypocyst.
8
9

10 660 Lewis et al. (1999) incubated and obtained cultures from cysts assignable to
11
12 661 *Spiniferites membranaceus* and recorded a distinctive motile stage. Further incubation
13
14 662 and culturing studies by Ellegaard et al. (2003) allowed details of the morphology to be
15
16 663 added, along with molecular phylogenetic analysis. Rather than describe this as a new
17
18 664 non-fossil species, Ellegaard et al. (2003) chose to emend *Spiniferites membranaceus* to
19
20 665 include characteristics of the motile stage and transfer the species to *Gonyaulax*, as
21
22 666 *Gonyaulax membranacea*. The approach taken here is to sustain the combination
23
24 667 *Spiniferites membranaceus* for the fossil cysts and to establish *Gonyaulax lewisiae* n. sp.
25
26 668 as the equivalent non-fossil species.
27
28
29

30 669

31 670

32 671 **Acknowledgements**

33 672

34
35 673 We are most grateful to N. Van Nieuwenhove for providing photos of *Spiniferites*
36
37 674 *elongatus* (Plate 1, figs. 1–4). MJH acknowledges support from a Natural Sciences and
38
39 675 Engineering Research Council of Canada Discovery Grant. This is NRCan contribution
40
41 676 number xxxxxxx. KNM acknowledges support from the PHENOMAP project, funded by
42
43 677 French National Research Agency (ANR) under grant ANR-20-CE02-0025.
44
45
46
47
48
49
50

51 678

52 679

1
2
3 680
4

5 681
6

7
8 682 **Disclosure statement**
9

10 683

11
12 684 No potential conflict of interest was reported by the authors.
13

14 685
15

16 686
17

18
19 687 **Notes on contributors**
20

21 688
22

23
24 689 MARTIN J. HEAD is a professor of Earth Sciences at Brock University. His interests are
25

26 690 in late Cenozoic marine palynology, and particularly the late Neogene–Quaternary
27

28 691 record of dinoflagellate cysts and acritarchs and their application to paleoenvironmental
29

30 692 reconstruction. He is also interested in formal chronostratigraphy including that of the
31

32 693 Quaternary Period, and is currently involved in efforts to formalize the Anthropocene.
33

34 694 He is a former president of AASP – The Palynological Society and of the Canadian
35

36 695 Association of Palynologists.
37

38 696
39

40
41
42 697 KENNETH NEIL MERTENS is a researcher at Ifremer, LER BO, Concarneau, France.
43

44 698 He received his Ph.D. in 2009 from Ghent University. His research interests are the
45

46 699 taxonomy, evolution, phylogeny and biogeography of dinoflagellates, and the
47

48 700 palaeoceanographical application of dinoflagellate cysts, particularly in the Quaternary
49

50 701 and Neogene.
51

52 702
53
54
55
56
57
58
59
60

1
2
3 703 ROBERT A. FENSOME is a research scientist with the Geological Survey of Canada
4
5 704 (GSC), part of the federal department of Natural Resources Canada, in their Atlantic
6
7 705 Division at the Bedford Institute of Oceanography, Dartmouth, Nova Scotia. During his
8
9 706 39-year tenure at the GSC, Rob has focussed mainly on Mesozoic and Cenozoic
10
11 707 dinoflagellate cysts from offshore eastern Canada, but recently ventured into projects
12
13 708 involving assemblages from north-western and Arctic Canada. While his mandate has
14
15 709 involved primarily biostratigraphical and palaeoenvironmental studies, he also has a
16
17 710 strong interest in dinoflagellate taxonomy and evolution, miospore taxonomy and
18
19 711 geological outreach, co-authoring and co-editing two books for a general audience, one
20
21 712 on the geology of Canada and one on the geology of Canada's Maritime Provinces.
22
23
24
25

26 713

27 714

28
29
30
31 715 **References**

32 716

33
34
35 717 Adl SM, Simpson AGB, Farmer MA, Andersen RA, Anderson OR, Barta, JR, Bowser
36
37 718 SS, Brugerolle G, Fensome RA, Fredericq S, et al. 2005. The new higher level
38
39 719 classification of eukaryotes with emphasis on the taxonomy of protists. *Journal of*
40
41 720 *Eukaryotic Microbiology*. 52:399–451.
42
43

44 721

45
46
47 722 Adl SM, Bass D, Lane CE, Lukeš J, Schoch CL, Smirnov A, Agatha S, Berney C, Brown
48
49 723 MW, Burki F, et al. 2019. Revisions to the classification, nomenclature, and diversity of
50
51 724 eukaryotes. *Journal of Eukaryotic Microbiology*. 66:4–119.
52

53 725
54
55
56
57
58
59
60

- 1
2
3 726 Bujak JP. 1980. V. Dinoflagellate cysts and acritarchs from the Eocene Barton Beds of
4
5 727 southern England. In: Bujak JP, Downie C, Eaton GL, Williams GL. Dinoflagellate cysts
6
7 728 and acritarchs from the Eocene of southern England. Special Papers in Palaeontology.
8
9
10 729 24:36–91.
11
12 730
13
14 731 Bütschli O. 1885. Dinoflagellata. In: Abtheilung II Mastigophora Bronn HG (editor),
15
16 732 Protozoa. Die Klassen und Ordnungen des Thier-Reichs, wissenschaftlich dargestellt in
17
18 733 Wort und Bild. CF Winter'sche Verlagshandlung, Leipzig. Heidelberg, p. 906–1029.
19
20
21 734
22
23 735 Chadeaud, M. 1950. Les cellules nageuses des algues dans l'embranchement des
24
25 736 Chromophycées. Comptes rendus hebdomadaires des séances de l'Académie des
26
27 737 Sciences. 231:788–790.
28
29
30 738
31
32 739 Claparède E, Lachmann, J. 1859. Études sur les infusoires et les rhizopodes. Institut
33
34 740 national génevois, Mémoires 6 (Mémoire 1):261–482. (Cover date 1858, issue date 1859,
35
36 741 according to Loeblich Jr. and Loeblich III, 1966.)
37
38
39 742
40
41 743 Davey RJ, Williams GL. 1966. IV. The genera *Hystriosphæra* and *Achomosphaera*.
42
43 744 In: Davey RJ, Downie C, Sarjeant WAS, Williams GL, Studies on Mesozoic and
44
45 745 Cainozoic dinoflagellate cysts. British Museum (Natural History) Geology, Bulletin,
46
47 746 Supplement. 3:28–52.
48
49
50 747
51
52
53
54
55
56
57
58
59
60

- 1
2
3 748 Deflandre G. 1937. Microfossiles des silex crétacés. Deuxième partie. Flagellés incertae
4
5 749 sedis. Hystrichosphaeridés. Sarcodinés. Organismes divers. Annales de paléontologie.
6
7 750 26:51–103 (al. 3–55), pl. 11–18 (al. pl. 8–15).
8
9 751
10
11 752 de Vernal A, Radi T, Zaragosi S, Van Nieuwenhove N, Rochon A, Allan E, De Schepper
12
13 753 S, Eynaud F, Head MJ, Limoges A, Londeix L, Marret F, Matthiessen J, Penaud A,
14
15 754 Pospelova V, Price A, Richerol T. 2020. Distribution of common modern dinoflagellate
16
17 755 cyst taxa in surface sediments of the Northern Hemisphere in relation to environmental
18
19 756 parameters: The new n=1968 database. Marine Micropaleontology. 159:101796, 1–23.
20
21 757
22
23 758 Diesing KM. 1866. Revision der Prothelminthen. Abtheilung: Mastigophoren.
24
25 759 Sitzungsberichte der Kaiserlichen Akademie der Wissenschaften. Mathematisch-
26
27 760 naturwissenschaftliche Classe. Abt. I. 52:287–401.
28
29 761
30
31 762 Dodge JD. 1989. Some revisions of the family Gonyaulacaceae (Dinophyceae) based on
32
33 763 a scanning electron microscope study. Botanica Marina. 32:275–298.
34
35 764
36
37 765 Ehrenberg CG. 1837. Über das Massenverhältniss der jetzt lebenden Kiesel-Infusorien
38
39 766 und über ein neues Infusorien-Conglomerat als Polirschiefer von Jastraba in Ungarn.
40
41 767 Abhandlungen der Königlichen Akademie der Wissenschaften zu Berlin, aus dem Jahre
42
43 768 1836, Physikalische Klasse, p. 109–135, pl. 1–2. [Published in the journal in 1838, but as
44
45 769 a separate in December 1837].
46
47 770
48
49
50
51
52
53
54
55
56
57
58
59
60

- 1
2
3 771 Ellegaard M, Daugbjerg N, Rochon A, Lewis J, Harding I. 2003. Morphological and
4
5 772 LSU rDNA sequence variation within the *Gonyaulax spinifera*–*Spiniferites* group
6
7 773 (Dinophyceae) and proposal of *G. elongata* comb. nov. and *G. membranacea* comb. nov.
8
9 774 *Phycologia*. 42(2):151–164.
10
11
12 775
13
14 776 Ellegaard ME, Head MJ, Versteegh GJM. 2018. Linking biological and geological data
15
16 777 on dinoflagellates using the genus *Spiniferites* as an example: the implications of species
17
18 778 concepts, taxonomy and dual nomenclature. *Palynology*. 42(supplement 1):221–230.
19
20 779
21
22
23 780 Evitt WR. 1985. Sporopollenin dinoflagellate cysts: their morphology and interpretation.
24
25 781 American Association of Stratigraphic Palynologists, Monograph Series. 1, 333 p.
26
27 782
28
29
30 783 Fensome RA, Taylor FJR, Norris G, Sarjeant WAS, Wharton DI, Williams GL. 1993. A
31
32 784 classification of living and fossil dinoflagellates. *Micropaleontology Special Publication*.
33
34 785 7:1–351.
35
36 786
37
38
39 787 Fensome RA, Williams GL, MacRae RA. 2019. The Lentin and Williams index of fossil
40
41 788 dinoflagellates 2019 edition. *AASP Contributions Series*. 50:1–1173.
42
43 789
44
45
46 790 Gaarder KR. 1954. Coccolithineae, Silicoflagellatae, Pterospermaceae and other forms
47
48 791 from the Michael Sars North Atlantic Deep-Sea Expedition 1910. Report on the
49
50 792 Scientific Results of the “Michael Sars” North Atlantic Deep-Sea Expedition 1910,
51
52 793 University of Bergen, John Grieg, Bergen 2(4):1–20 + Tabl. 1–5.
53
54
55
56
57
58
59
60

- 1
2
3 794
4
5 795 Gómez F. 2012. A checklist and classification of living dinoflagellates (Dinoflagellata,
6
7 796 Alveolata). *CICIMAR Océánides*. 27(1):65–140.
8
9
10 797
11
12 798 Gravendyck J, Fensome RA, Head MJ, Herendeen PS, Riding JB, Bachelier JB, Turland
13
14 799 NJ. 2021. Taxonomy and nomenclature in palaeopalynology: basic principles, current
15
16 800 challenges and future perspectives. *Palynology*. 45(4):717–743.
17
18
19 801
20
21 802 Gurdebeke PR, Mertens KN, Bogus K, Marret F, Chomérat N, Vrielinck H, Louwye S.
22
23 803 2018. Taxonomic re-investigation and geochemical characterization of Reid’s (1974)
24
25 804 species of *Spiniferites* from holotype and topotype material. *Palynology*. 42, supplement
26
27 805 1:93–110.
28
29
30 806
31
32 807 Harland R, Reid PC, Dobell P, Norris G. 1980. Recent and sub-Recent dinoflagellate
33
34 808 cysts from the Beaufort Sea, Canadian Arctic. *Grana*. 19:211–225.
35
36
37 809
38
39 810 Head MJ. 1996. Modern dinoflagellate cysts and their biological affinities. In: Jansonius
40
41 811 J, McGregor DC, editors. *Palynology: principles and applications*. American Association
42
43 812 of Stratigraphic Palynologists Foundation, Dallas, Texas, vol. 3, p. 1197–1248.
44
45
46 813
47
48 814 Head MJ, Fensome RA, Herendeen PS, Skog JE. 2016. (315–319) Proposals to amend
49
50 815 Article 11.8 and its Examples to remove ambiguity in the sanctioning of dual
51
52
53
54
55
56
57
58
59
60

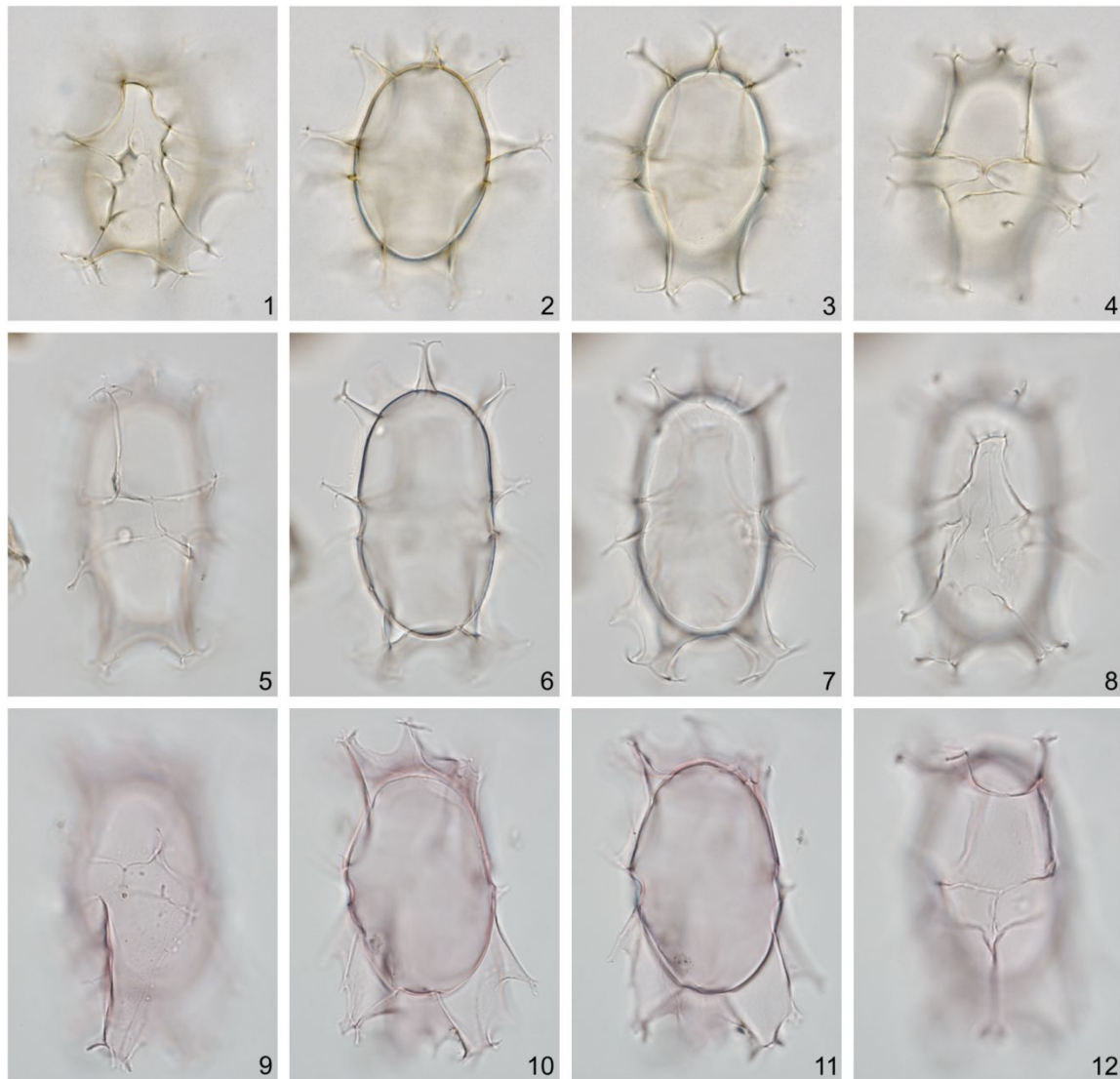
- 1
2
3 816 nomenclature for dinoflagellates, and an emendation of Article 11.7, Example 29. Taxon.
4
5 817 65:902–903.
6
7
8 818
9
10 819 Head MJ, Mertens KN, Fensome RA, submitted. Dual nomenclature in organic-walled
11
12 820 dinoflagellate cysts I: concepts, methods and applications. Palynology.
13
14
15 821
16
17 822 Kofoid CA. 1911. Dinoflagellata of the San Diego region, IV. The genus *Gonyaulax*,
18
19 823 with notes on its skeletal morphology and a discussion of its generic and specific
20
21 824 characters. University of California Publications in Zoology. 8:187–286.
22
23
24 825
25
26 826 Lemmerman E. 1903. Das Phytoplankton des Meeres. II. Beitrag. Abhandlungen
27
28 827 herausgegeben vom Naturwissenschaftlichen Verein zu Bremen. 17, 341–418.
29
30
31 828
32
33 829 Lewis J, Rochon A, Harding I. 1999. Preliminary observations of cyst-theca relationships
34
35 830 in *Spiniferites ramosus* and *Spiniferites membranaceus* (Dinophyceae). Grana. 38:113–
36
37 831 124.
38
39
40 832
41
42 833 Lewis J, Rochon A, Ellegaard M, Mudie P, Harding I. 2001. The cyst-theca relationship
43
44 834 of *Bitectatodinium tepikiense* (Dinophyceae). European Journal of Phycology. 36:137–
45
46 835 146.
47
48
49 836
50
51 837 Lindemann E. 1928. Abteilung Peridineae (Dinoflagellatae). In: Engler, A, editor. Die
52
53 838 natürlichen Pflanzenfamilien nebst ihren Gattungen und wichtigeren Arten insbesondere

- 1
2
3 839 den Nutzpflanzen. Zweite stark vermehrte verbesserte Auflage Band. 2. Verlag Wilhelm
4
5 840 Engelmann, Leipzig, p. 3–104.
6
7
8 841
9
10 842 Lohmann H. 1904. Eier und sogenannte Cysten der Plankton-Expedition. Anhang:
11
12 843 Cyphonautes. In: Ergebnisse der Plankton-Expedition der Humboldt-Stiftung. Band 4 N.
13
14 844 Lipsius and Tischer, Kiel and Leipzig.
15
16
17 845
18
19 846 Mantell GA. 1854. The Medals of Creation; or, First Lessons in Geology and the Study
20
21 847 of Organic Remains; Second Edition. 930 p., 6 pl. (in two volumes); Henry G. Bohn,
22
23 848 London, U.K.
24
25
26 849
27
28 850 Matsuoka K. 1983. Late Cenozoic dinoflagellates and acritarchs in the Niigata district,
29
30 851 central Japan. *Palaeontographica, Abteilung B.* 187:89–154, pl. 1–15.
31
32
33 852
34
35 853 Matsuoka K, Bujak JP. 1988. Cenozoic dinoflagellate cysts from the Navarin Basin,
36
37 854 Norton Sound and St. George Basin, Bering Sea. *Bulletin of the Faculty of Liberal Arts,*
38
39 855 *Nagasaki University, Natural Science.* 29 (1):1–147.
40
41
42 856
43
44 857 Matzenauer L. 1933. Die Dinoflagellaten des Indischen Ozeans. *Botanisches Archiv.*
45
46 858 35(4):437–510.
47
48
49 859
50
51 860 Mertens KN, Carbonell-Moore C. 2018. Introduction to *Spiniferites* Mantell 1850 special
52
53 861 issue. *Palynology.* 42(S1):1–9.
54
55
56
57
58
59
60

- 1
2
3 862
4
5 863 Mertens KN, Van Nieuwenhove N, Gurdebeke PR, Aydin H, Bogus K, Bringué M, Dale
6
7
8 864 B, De Schepper S, de Vernal A, Ellegaard M, Grothe A, Gu H, Head MJ, Heikkilä M,
9
10 865 Limoges A, Londeix L, Louwye S, Marret F, Masure E, Matsuoka K, Mudie PJ, Penaud
11
12 866 A, Pospelova V, Price AM, Ribeiro S, Rochon A, Sangiorgi F, Schreck M, Torres V,
13
14 867 Uzar S, Versteegh GJM, Warny S, Zonneveld K. 2018. The dinoflagellate cyst genera
15
16 868 *Achomosphaera* Evitt 1963 and *Spiniferites* Mantell 1850 in Pliocene to modern
17
18 869 sediments: a summary of round table discussions. *Palynology*. 42: supplement 1:10–44.
19
20
21 870
22
23
24 871 Parke M, Boalch GT, Jowett R, Harbour DS. 1978. The genus *Pterosperma*
25
26 872 (Prasinophyceae): species with a single equatorial ala. *Journal of the Marine Biological*
27
28 873 *Association, U.K.* 58:239–276.
29
30
31 874
32
33 875 Pascher A. 1914. Über Flagellaten und Algen. *Berichte der Deutschen Botanischen*
34
35 876 *Gesellschaft*. 32(2):136–160.
36
37
38 877
39
40 878 Pouchet G. 1894. Histoire naturelle. In: Voyage de “La Manche” a l’Ile Jan Mayen et au
41
42 879 Spitzberg (juillet–août 1892). *Nouvelles Archives des Missions Scientifiques et*
43
44 880 *Littéraires*. 5(10):155–217.
45
46
47 881
48
49 882 Reid PC. 1974. Gonyaulacacean dinoflagellate cysts from the British Isles. *Nova*
50
51 883 *Hedwigia*. 25:579–637.
52
53
54 884
55
56
57
58
59
60

- 1
2
3 885 Rossignol M. 1964. Hystrichosphères du Quaternaire en Méditerranée orientale, dans les
4
5 886 sédiments Pléistocènes et les boues marines actuelles. *Revue de micropaléontologie*.
6
7 887 7:83–99.
8
9 888
10
11 889 Sarjeant WAS. 1970. The genus *Spiniferites* Mantell, 1850 (Dinophyceae). *Grana*.
12
13 890 10:74–78.
14
15 891
16
17 892 Taylor FJR. 1980. On dinoflagellate evolution. *BioSystems*. 13:65–108.
18
19 893
20
21 894 Van Nieuwenhove N, Potvin É, Heikkilä M, Pospelova V, Mertens KN, Masure E,
22
23 895 Kucharska M, Eun Jin Yang, Chomérat N, Zajaczkowski M. 2018. Taxonomic revision
24
25 896 of *Spiniferites elongatus* (the resting stage of *Gonyaulax elongata*) based on
26
27 897 morphological and molecular analyses. *Palynology*. 42, S1:111–134.
28
29 898
30
31 899 Van Nieuwenhove N, Head MJ, Limoges A, Pospelova V, Mertens KN, Matthiessen J,
32
33 900 De Schepper S, de Vernal A, Eynaud F, Londeix L, Marret F, Peynaud A, Radi T,
34
35 901 Rochon A. 2020. An overview and brief description of common marine organic-walled
36
37 902 dinoflagellate cyst taxa occurring in surface sediments of the Northern Hemisphere.
38
39 903 *Marine Micropaleontology*. 159:101814:1–46.
40
41 904
42
43 905 Wall D, Dale B. 1968. Modern dinoflagellate cysts and evolution of the Peridiniales.
44
45 906 *Micropaleontology*. 14:265–304.
46
47 907
48
49
50
51
52
53
54
55
56
57
58
59
60

- 1
2
3 908 Zonneveld KAF, Marret F, Versteegh GJM, Bogus K, Bonnet S, Bouimetarhan I, Crouch
4
5 909 E, de Vernal A, Elshanawany R, Edwards L, Esper O, Forke S, Grøsfjeld K, Henry M,
6
7 910 Holzwarth U, Kieft J-F, Kim S-Y, Ladouceur S, Ledu D, Chen L, Limoges A, Londeix
8
9
10 911 L, Lu SH, Mahmoud MS, Marino G, Matsouka K [sic], Matthiessen J, Mildenhall DC
11
12 912 [sic], Mudie P, Neil HL, Pospelova V, Qi Y, Radi T, Richerol T, Rochon A, Sangiorgi F,
13
14 913 Solignac S, Turon J-L, Verleye T, Wang Y, Wang Z, Young M. 2013. Atlas of modern
15
16 914 dinoflagellate cyst distribution based on 2405 data points. Review of Palaeobotany and
17
18
19 915 Palynology. 191:1–197.
20
21 916
22
23
24 917 Plate captions
25
26 918
27
28
29
30
31
32
33
34
35
36
37
38
39
40
41
42
43
44
45
46
47
48
49
50
51
52
53
54
55
56
57
58
59
60

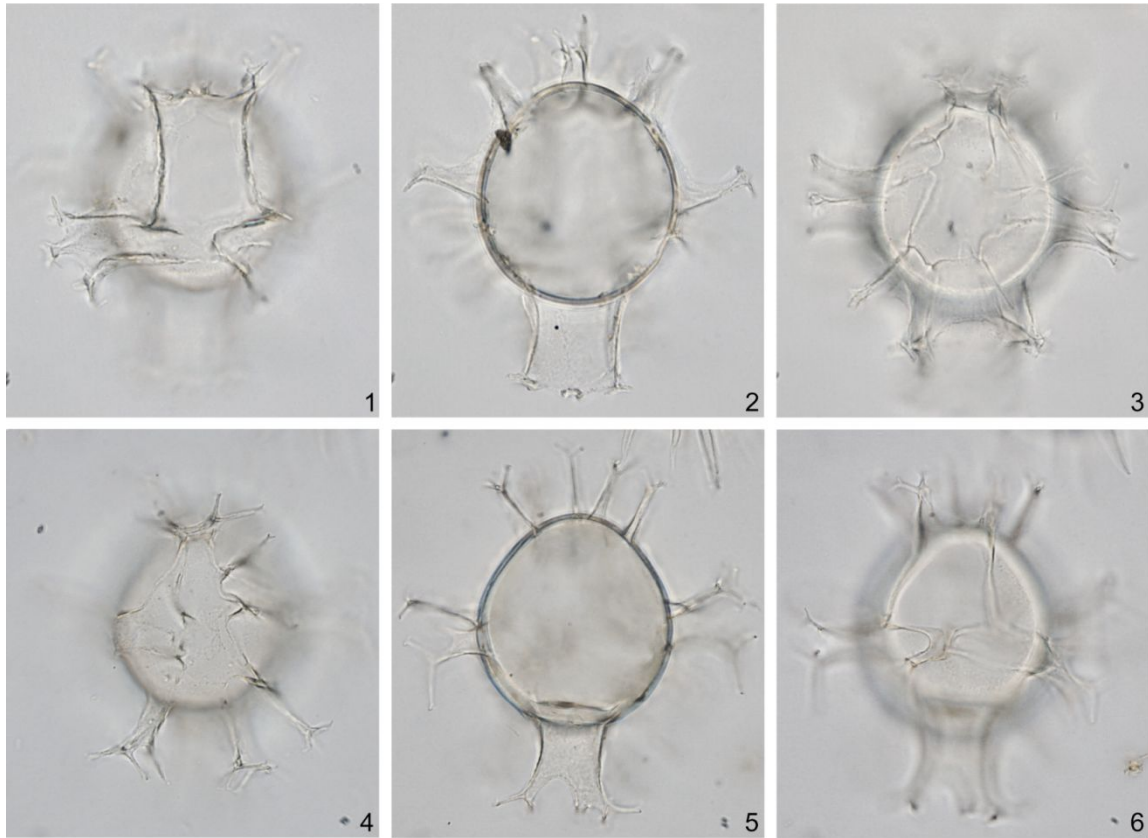


919

920 Plate 1. *Spiniferites elongatus* Reid 1974; 1–4 *Spiniferites elongatus* s.l., ventral view at
 921 high to low foci; upper Quaternary of the Iceland Plateau, core DANA12-11/2-GC01;
 922 central body length 48 μm (from plate 13, figs. 1, 3–5 of Van Nieuwenhove et al., 2020;
 923 photos by Nicolas Van Nieuwenhove). 5–8 *Spiniferites elongatus* forma *elongatus*
 924 (autonym), dorsal view at high to low foci; Holocene of the continental slope off Nova
 925 Scotia, core MD2033, 395–396 cm, slide 2, H50/2; central body length 59 μm (photos by
 926 MJH). 9–12 *Spiniferites elongatus* forma *frigidus* n. stat., right lateroventral view at high

1
2
3 927 to low foci; Holocene of the continental slope off Nova Scotia, core MD2033, 215–216
4
5 928 cm, slide 5, D45/1; central body length 50 μm (photos by MJH).

6
7
8 929



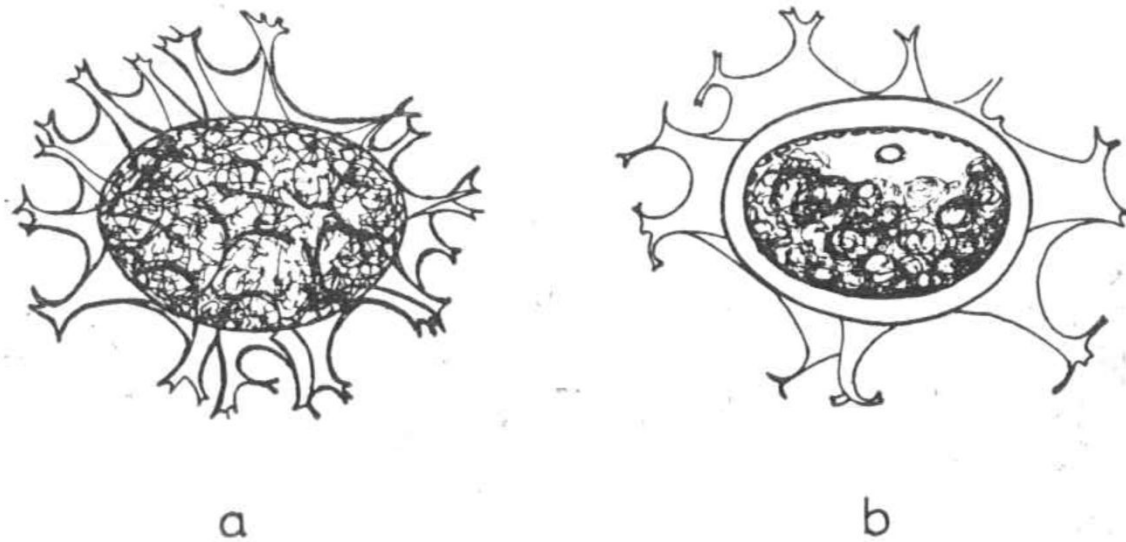
36
37 931 Plate 2. *Spiniferites membranaceus* (Rossignol 1964) Sarjeant 1970 from Quaternary
38
39 932 sediments off Portugal. 1–3 dorsal view at high to low focus, central body length 31 μm .
40
41 933 4–6 ventral view of a different specimen at high to low focus, central body length 32 μm .
42
43
44 934 From plate 15, figs. 1–6 of Van Nieuwenhove et al. (2020). Photos by KNM.

45
46 935

47
48 936

49
50
51 937 Figure captions

52
53 938



939

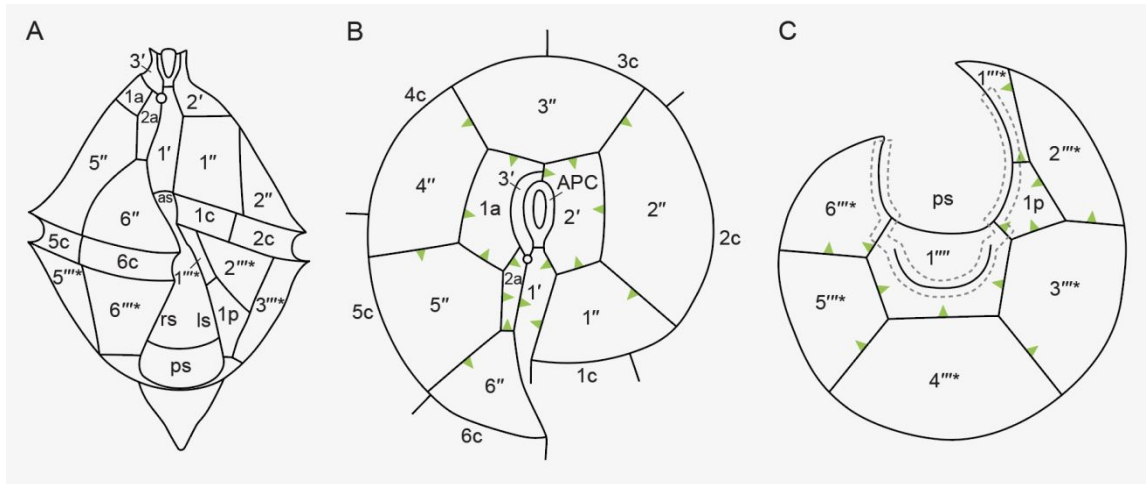
940 Figure 1. *Gonyaulax ovum* (Gaarder 1954) n. comb., emend., showing the two specimens
941 of *Pterosperma ovum* illustrated by Gaarder 1954, her figure 19; both from Station 3
942 south of Ireland. a, surface view, cell length 38 μm ; b, longitudinal cross-section, cell
943 length 47 μm ; illustration designated here as the holotype; note thick endospore and cell
944 contents as well as the diagnostic outline. Gaarder (1954) did not specify a holotype, but
945 this was not required prior to 1958. *Gonyaulax ovum* was collected from the water
946 column and, although typified by a cyst, must be considered a non-fossil species. Its
947 equivalent fossil-species is *Spiniferites elongatus*.

948

949

950

951



952

953 Figure 2. Schematic drawing of motile cell of *Gonyaulax ovum* (Gaarder 1954) n. comb.,

954 emend. showing details of tabulation on the motile cell. A, ventral view, B, apical view,

955 and C, antapical view with dashed line indicating the position and maximum extent of

956 antapical flanges (lists). Modified kofoidian plate labeling includes: APC = apical pore

957 complex, vp = ventral pore; and sulcal plates, as = anterior, rs = right, ls = left, ps =

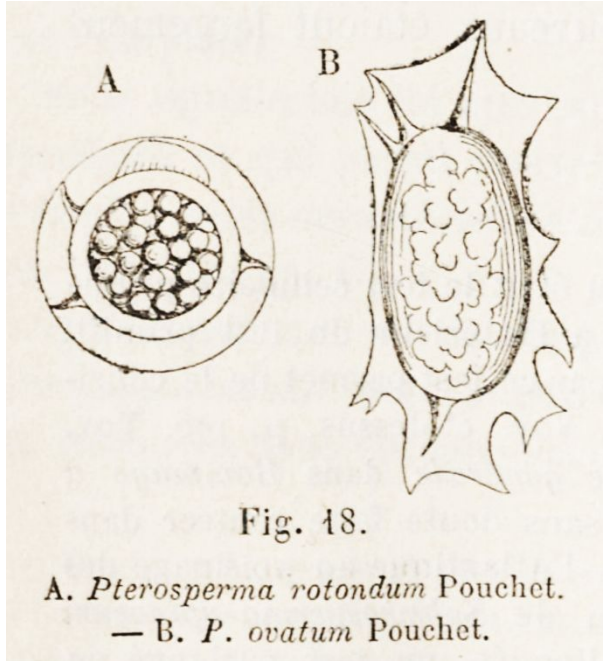
958 posterior. The first postcingular homolog (1'''*) is designated as such because it lies

959 within the sulcus. Plate overlap direction is indicated by green arrowheads. Modified

960 from figs. 1–3 of Ellegaard et al. (2003), as *Gonyaulax elongata*.

961

962



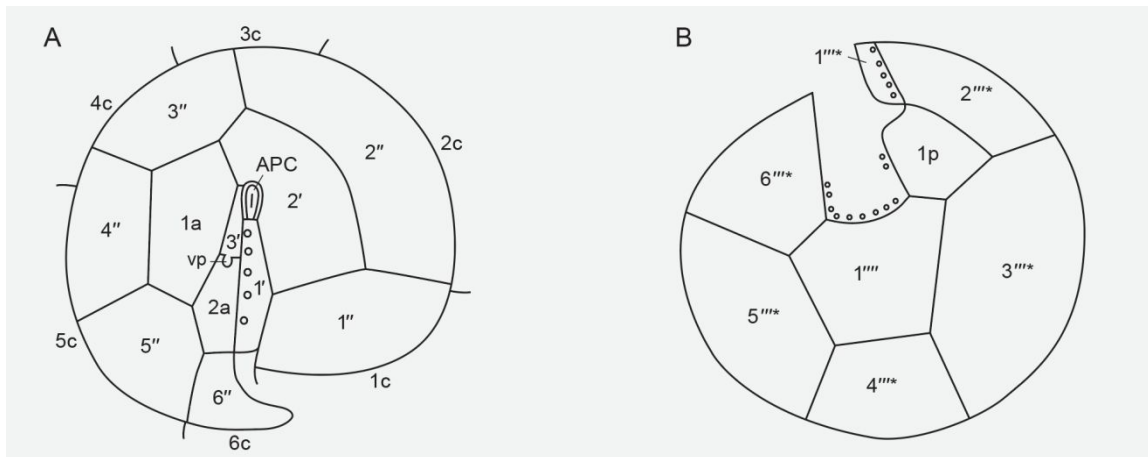
963

964

965 Figure 3. The types of *Pterosperma rotundum* Pouchet 1894 and *Pterosperma ovatum*
 966 Pouchet 1894 (now *Trochiscia ovata*) reproduced from Pouchet 1894, fig. 18a and fig.
 967 18b respectively. *Pterosperma ovatum* bears superficially resemblance to *Spiniferites*
 968 *elongatus*. No scale was given by Pouchet (1894).

969

970



971

1
2
3 972 Figure 4. *Gonyaulax lewisiae* n. sp. showing details of tabulation on the motile cell. 1,
4
5 973 apical view, and 2, antapical view with dashed line indicating the position and maximum
6
7 974 extent of antapical flanges (lists). Modified kofoidian plate labeling includes: APC =
8
9
10 975 apical pore complex, vp = ventral pore. The first postcingular homolog (*1'') is
11
12 976 designated as such because it lies within the sucus. From fig. 20c, 20d of Lewis et al.
13
14 977 (1999), as *Spiniferites membranaceus* motile cells.
15
16
17 978
18
19
20
21
22
23
24
25
26
27
28
29
30
31
32
33
34
35
36
37
38
39
40
41
42
43
44
45
46
47
48
49
50
51
52
53
54
55
56
57
58
59
60