



Article title: Recent proposals on nomenclature of dinoflagellates (Dinophyceae)

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Recent proposals on nomenclature of dinoflagellates (Dinophyceae)

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28 **Abstract**

29 The recent proposals to conserve or reject dinoflagellate names are commented. The
30 Nomenclatural Committee for Algae (NCA) recommended to conserve *Scrippsiella*
31 against *Heteraulacus* and *Goniodoma* (proposal #2382). The synonymy of *Peridinium*
32 *acuminatum* and *Glenodinium trochoideum* is highly questionable, and one Stein's
33 illustration of *Goniodoma acuminatum* as type will solve the doubts. An alternative genus
34 and family name for the gonyaulacoid taxa formerly classified in *Goniodoma* is not
35 provided, and *Scrippsiella* is a junior synonym of *Duboscquodinium*. The NCA
36 confirmed *Amphidoma acuminata* as type species against *A. nucula* (2577). Stein
37 established *Amphidoma nucula* as the representative species of the genus, and the poor-
38 defined *A. acuminata* is associated with higher 'nomenclatural instability' because it is
39 probably a *Centrodinium* species. The NCA recommended *Heterocapsa steinii* as type of
40 *Heterocapsa* (2607). That species name is a junior synonym of *Properidinium*
41 *heterocapsum* and *Peridinium monas*. That taxon and allied species should be placed in
42 *Cachonina* because Stein proposed *Heterocapsa* for three species of the
43 Kryptoperidiniaceae. The proposal to conserve *Alexandrium* against *Blepharocysta*
44 (2686) is based on that *Peridinium splendor-maris* is a senior synonym of *Alexandrium*
45 *balechii*, currently classified in *Gessnerium*. *Peridinium splendor-maris* is a collective
46 name that includes undefined organisms, and no description or illustration corresponded
47 to *Alexandrium* or *Gessnerium*. The NCA reported that *Alexandrium catenella* and *A.*
48 *fundyensis* are synonyms, without comments on *A. pacificum* (2302). The consequence is
49 that one of the five species of that group has not name. Naming taxa should follow the
50 principle of priority and the article 7.3 of the International Code of Nomenclature for
51 algae, fungi, and plants, and rejection or conservation of names should be exceptional.
52 Based on a supposed 'nomenclatural stability', the NCA is creating arbitrariness and
53 instability in naming dinoflagellate taxa based on questionable taxonomical
54 interpretations.

55

56 **Keywords:** *Alexandrium*, dinoflagellates, Dinophyta, *Heterocapsa*, *Kryptoperidinium*,
57 nomenclature, *Scrippsiella*, systematics, taxonomy

58 **Abbreviations:** *auct. mult.*: *auctorum multorum*. Subsequent authors used a name in a
59 different sense to the original author. ICN, International Code of Nomenclature for algae,
60 fungi, and plants; INA, *Index Nominum Algarum*; NCA, Nomenclatural Committee for
61 Algae; *s.l.*, *sensu lato*; *s.s.*, *sensu stricto*.

62 **1. Introduction**

63 Dinoflagellates are unicellular organisms with ~2500 correct species (Gómez 2012a).
64 About one half of the taxa are heterotrophic, but this percentage could be higher because
65 the descriptions of heterotrophic species receive less attention (Gómez 2012b).
66 Dinoflagellates are phylogenetically related to the apicomplexans (i.e., agent of the
67 malaria) and the ciliates, and distantly related to plants, fungi or algae. In the last decades
68 nearly all the dinoflagellate taxonomical innovations follow the rules and
69 recommendations of the International Code of Nomenclature for algae, fungi, and plants
70 (ICN, Turland et al. 2018). Charles Atwood Kofoid and Enrique Balech, two of the most
71 prolific authors, described new dinoflagellate taxa as zoologists. The names need only
72 satisfy the requirements of the International Code of Zoological Nomenclature (ICN, Art.
73 45.1). Some contemporaneous authors consider the dinoflagellates as ambiregnal
74 (protozoa and algae) proposing names using the Zoological Nomenclature (Özdikmen
75 2009, Nakada 2010).

76 Dinoflagellates are unicellular organisms, and most of the species have not rigid
77 covering. This makes difficult the conservation of the type specimens. Due to the especial
78 characteristics of these microscopic groups, the ICN has more flexible rules in the
79 conservation of the type material, and published illustrations are accepted as type (ICN,
80 art. 40.5). Due to the poor optical resolution of the earlier microscopes, the identity of
81 numerous taxa described in the 19th century are doubtful due to the unrealism and/or
82 scarcely detail of the original illustrations. Other difficulty is that sometimes the
83 illustrations were never published. Consequently, authors based exclusively on the
84 diagnoses may have discrepancies on the interpretation of the taxa identities. This is a
85 subjective part of the taxonomy where each author has his/her own criteria in the
86 interpretation of the diagnoses and available original illustrations. The publication in
87 taxonomical journals of new interpretations of the identity and synonymy of these earlier
88 dinoflagellates do not mean that these are fortunate. Each researcher must evaluate the
89 scientific evidences. This requires experience on dinoflagellate taxonomy in order to
90 interpret the line drawings of the original descriptions, and the style of the earlier
91 microscopists.

92

93 **2. Earlier dinoflagellate descriptions**

94 The earliest illustration of a dinoflagellate corresponds to *Noctiluca scintillans*, an
95 aberrant dinoflagellate visible with the naked eye due to its large size, bioluminescent and

96 responsible of red tides in the coastal waters of Europe (where the first microscopes were
97 available). Several common species of the current genera *Ceratium* and *Tripos* were later
98 described (Müller 1776, Schrank 1793). One of the most prolific earlier microscopists
99 was Christian Gottfried Ehrenberg (1795–1876). His abundant materials and illustrations
100 are conserved at the Ehrenberg's collection in the Museum of Natural History at Berlin.
101 Ehrenberg's drawings were scanned, labelled with the code 'ECdraw' followed by a
102 number, and available online.

103 Ehrenberg proposed six genera and twenty-four species of extant dinoflagellates
104 that are currently in use. Other species cannot be assigned with certainty to known
105 dinoflagellates due to the scarce detail or even unrealistic structures in the illustrations
106 (i.e., *Peridinium delitiense*, ECdraw943). In addition to the problems for accessing to the
107 literature in the first half of the 19th century, Ehrenberg added the dispersion of the
108 information of his taxonomical innovations in distinct publications. For example, his new
109 taxa could be cited as *nomen nudum* in a publication, a short diagnosis may appear years
110 later in another publication, and the illustrations were published years, even decades, after
111 the diagnoses. Minor matters are the discrepancies in the cover and issue date year of
112 publication (i.e., Farr et al. 1979, p. 1290). The illustrations are sometimes reported in a
113 plate with numerous other drawings that looks like to play with where's Wally/Waldo
114 wallpapers (i.e., Mikrogeologie). Illustrations are useful to identify the species, but they
115 are not a requirement to consider a name as validly published. The type of a dinoflagellate
116 may be an effectively published illustration, but this was applicable for taxa described
117 after 1957 (ICN, art. 40.1). Then, the absence or difficulties to access to the original
118 illustration is not a requirement for the valid publication of Ehrenberg's taxa in the 19th
119 century. More important is the ICN article 38.1, "In order to be validly published, a name
120 of a new taxon must be accompanied by a description or diagnosis of the taxon".
121 Ehrenberg's diagnoses are often short, or restricted to a comment in the text. Then, it is
122 questionable whether Ehrenberg's descriptions satisfied the requirements (ICN, art. 38.4).

123 Claparède and Lachmann (1859), and Stein (1883) identified Ehrenberg's taxa based
124 on the interpretation of the short diagnoses. Present day, when these Ehrenberg's
125 illustrations are available online, we realize that the interpretations by Claparède and
126 Lachmann (1859) and Stein (1883), and followed by further generations of taxonomists,
127 were sometimes unfortunate. An example are the Ehrenberg's species of *Peridinium*
128 currently placed in the genus *Tripos* (Gómez 2021). A dilemma appears: to correct the

129 errors and to use the species names following Ehrenberg, or to maintain the errors
130 avoiding changes because Ehrenberg' species names are basionyms of new combinations
131 and types of genera of common use. The ICN article 7.3 states, "A new combination or a
132 name at new rank is typified by the type of the basionym even though it may have been
133 applied erroneously to a taxon now considered not to include that type". Scientists must
134 be people prone to correct the errors and to propose the due changes. Authors such as Dr.
135 M. Gottschling and Dr. M. Elbrächter claiming on 'nomenclatural stability' submitted
136 proposals to conserve or reject names contrary to the principle of priority of the ICN and
137 the article 7.3. This study reviews the taxonomical bases of some of the recent and future
138 proposals.

139

140 **3. The case of *Peridinium acuminatum* and *Goniodoma***

141 (2382) Proposal to conserve the name *Scrippsiella* against *Heteraulacus* and *Goniodoma*
142 (Thoracosphaeraceae, Dinophyceae). Gottschling, M., Elbrächter, M. 2015. *Taxon* 64:
143 1051–1052. Recommended (Prud'homme van Reine 2017)

144 (2383) Proposal to reject the name Goniodomataceae (Dinophyceae). Elbrächter, M.,
145 Gottschling, M. (2015). *Taxon* 64: 1052–1053. Recommended (Prud'homme van Reine
146 2017)

147

148 **3.1. Antecedents**

149 Ehrenberg (1834, 541, 575, t. II, fig. 5, 1836) described *Peridinium acuminatum* from the
150 Kiel fjord, Baltic Sea, with three illustrations (Fig. 1A). One illustration showed a cell
151 with a nearly hexagonal transversal section (apical or antapical view), and other two cells
152 with a polygonal contour in antero-posterior view. The shape of the hypotheca was an
153 isosceles trapezoid with a flat antapex, and the epitheca was angled, convex, and with
154 cuspidate apex (Fig. 1A, [ECdraw938](#)).

155 Diesing (1850, p. 100) transferred Ehrenberg's and SchmarDA's species of
156 *Peridinium* into the new genus *Heteraulacus* Diesing 1850. His first new combination
157 was *Heteraulacus fuscum* for *Peridinium fuscum* Ehrenberg 1834 (basionym of the type
158 species of the unarmoured dinoflagellate genus *Gymnodinium* F.Stein 1878), and the third
159 species was the armoured *Heteraulacus acuminatus*, citing *Peridinium acuminatum*

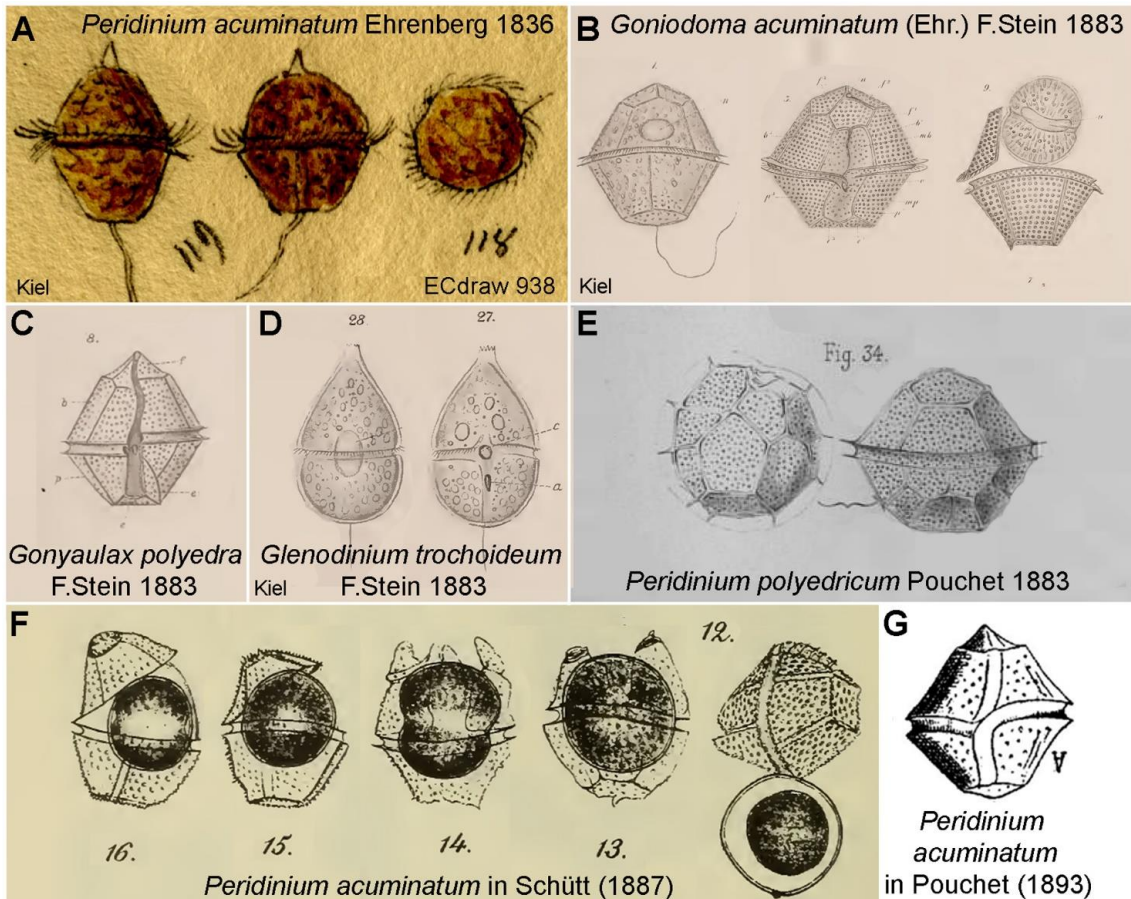
160 Ehrenberg 1836 as basionym. Later, Diesing (1866, p. 381) proposed *Heteroaulax*
161 Diesing, for *Peridinium* Ehrenberg and ‘*Heteroaulacus* Diesing pridem’ (*pridem* = prior).
162 It is uncertain why Diesing changed the spelling and proposed other new generic name
163 for species that he previously placed in *Heteroaulacus*. *Heteroaulax* is apparently a *nomen*
164 *vanum*. Diesing (1866) reported as first new combination *Heteroaulax adriaticus*
165 (Schmarda 1846) Diesing for *Peridinium adriaticum* Schmarda that is currently
166 considered an unarmoured dinoflagellate of *Gymnodinium*. The second species was
167 *Heteroaulax acuminatus*. It is common to assign the type species to the first described
168 species in a publication that proposed several congeneric species and the generitype is not
169 specified. For example, Stein (1883) proposed the genus *Podolampas* for *P. bipes* and *P.*
170 *palmipes*, and Loeblich and Loeblich (1966) fixed *P. bipes* as type that is the first
171 illustrated species by Stein. In the case of *Heteroaulacus*, Loeblich and Loeblich (1966)
172 fixed as type the third species name, the armoured *Heteroaulacus acuminatus*
173 (\equiv *Peridinium acuminatum* Ehrenberg) despite Diesing reported species of unarmoured
174 dinoflagellates currently placed in *Gymnodinium* F.Stein 1878 for his first new
175 combinations of *Heteroaulacus* and *Heteroaulax*. In the same publication, Loeblich and
176 Loeblich (1966) reported *Goniodoma* F.Stein 1883 with *Peridinium acuminatum*
177 Ehrenberg as basionym of the generitype. A.R. Loeblich and L. Loeblich, and Steidinger
178 transferred other species of gonyaulacoid dinoflagellates into *Heteroaulacus* such as
179 *Heteroaulacus depressus* (Gaarder) A.R.Loeblich, *H. ostensfeldii* (Paulsen) A.R.Loeblich,
180 *Heteroaulacus ostensfeldii* (Paulsen) A.R.Loeblich, *H. polyedricus* (C.H.G.Pouchet) Drugg
181 & Loeblich, *H. reticulatus* (Kofoid & Michener) Steidinger and *H. sphaericus* (G.Murray
182 & Whitting) A.R.Loeblich. The ICN article 10.5 regulates the designation of a type of a
183 name of a genus, but it is not easy due to the subjectivity of ‘largely mechanical method
184 of selection’. A discussion is available in the Report of the Nomenclature Committee for
185 Algae 22 concerning the proposal (2577) on *Amphidoma* (Andersen 2020). The NCA
186 supported the method of selection of multiple type species by Loeblich and Loeblich
187 (1966). This can be extrapolated to the case of *Heteroaulacus acuminatus* (\equiv *Peridinium*
188 *acuminatum* Ehrenberg) as type of the genus *Heteroaulacus*.

189 After Diesing (1850), Claparède and Lachmann (1859, p. 405) used the name
190 *Peridinium acuminatum* for a species responsible of blooms at Bergen fjord, Norway.
191 They reported the diagnosis, “*Peridinium ovoïde*... fort petits, ne dépassant guère 0mm,03
192 à 0,04 en longueur”. Claparède and Lachmann did not cite any illustration by Ehrenberg

193 and they did not report any illustration of their observations. Unequivocally Ehrenberg's
194 *Peridinium acuminatum* is not ovoid, and the details of Ehrenberg's illustrations suggest
195 that it is larger than Claparède and Lachmann's taxon.

196 **3.2. Stein's interpretation**

197 Samuel Friedrich Nathaniel Ritter von Stein (1818–1885) published a milestone study on
198 dinoflagellates in 1883. Ehrenberg (1834) described *Peridinium acuminatum* at Kiel, and
199 Stein (1883) illustrated it with more detail also from samples collected at Kiel. In addition
200 to the polygonal contour with a flat antapex, Stein (1883, p. 12–13) had better optical
201 resolution, and he illustrated the thick-plates with thecal pores that characterized that
202 species (Fig. 1B). Although Ehrenberg or Stein did not provide size measurements,
203 Stein's illustration of the surface ornamentation with poroids suggest that the species was
204 relatively large. It is evident that the small ovoid cell with smooth surface misidentified
205 as *Peridinium acuminatum* by Claparède and Lachmann (1859) is distinct from the
206 medium- or large sized cell with polygonal contour reported by Ehrenberg and Stein at
207 Kiel (Fig. 1A–B). Stein (1883) proposed a new genus for *Peridinium acuminatum* due to
208 the angled cell contour that contrasted with the rotund or ovoid contour of the other
209 species of Ehrenberg's genera *Glenodinium* or *Peridinium*. He proposed *Goniodoma*
210 F.Stein 1883 (non *Goniodoma* Zeller 1849, an insect). Stein (1883) knew Diesing's
211 publication (cited in his page 12) where *Heteraulacus acuminatus* was proposed for
212 *Peridinium acuminatum* Ehrenberg, but he proposed *Goniodoma acuminatum* for the
213 same taxon. Stein (1883) also proposed other gonyaulacoid dinoflagellate, *Gonyaulax*
214 *polyedra* F.Stein 1883 (Fig. 1C), with a shape close to *Peridinium acuminatum*
215 Ehrenberg.



216

217 **Fig. 1.** Line drawings of *Peridinium acuminatum*, *Glenodinium trochoideum* and
 218 *Gonyaulax polyedra*.

219

220 Stein (1883) also described the new species *Glenodinium trochoideum* ('trochus'=
 221 wheel, round) for a small cell with an ovoid contour, hemispherical hypotheca and
 222 epitheca tapering into an apex like a truncated horn (Fig. 1D). The thecal plates of this
 223 small species were hardly discernible, and lacked pores or other thecal ornamentation
 224 visible with the optical resolution at that time. *Glenodinium trochoideum* fit well with
 225 Claparède and Lachmann's diagnosis of *Peridinium acuminatum*, "Peridinium ovoïde, à
 226 carapace lisse, homogène, terminée en pointe en arrière". *Glenodinium trochoideum* was
 227 later transferred into *Peridinium*, and finally into *Scrippsiella* Balech 1959 as *S.*
 228 *trochoidea* (Balech) Loeblich 1976. In addition to the differences in size, *Goniiodoma*
 229 *acuminatum* (\equiv *Peridinium acuminatum*) possesses a polygonal or angled contour in the
 230 anterior-posterior view and in the transversal section (Fig. 1A–B), while and *Glenodinium*
 231 *trochoideum* has an oval contour in the anterior-posterior view, and a round transversal
 232 section (Fig. 1D). The apex of *Peridinium acuminatum* is acuminate, tapering to a point,

233 while the apex of *Glenodinium trochoideum* is tubular and truncate. *Peridinium*
234 *acuminatum* has marked polygonal plates ornamented with poroids, while *Glenodinium*
235 *trochoideum* showed a smooth surface and scarcely discernible plates. Unequivocally,
236 *Scrippsiella trochoidea* and *Goniodoma acuminatum* belong to distinct orders.

237 **3.3. Other observations of *Peridinium acuminatum***

238 Charles Henri Georges Pouchet (1833–1894) described *Peridinium polyedricum* from the
239 coast of Marseilles in the French Mediterranean Sea. Pouchet (1883) only illustrated the
240 dorsal and antapical views of the cell (Fig. 1E). This is problematic because the ventral
241 and apical views are more informative in dinoflagellate taxonomy. Despite these
242 deficiencies, unequivocally Stein 1883's *Goniodoma acuminatum* (Fig. 1B) and Pouchet
243 1883's *Peridinium polyedricum* (Fig. 1E) are conspecific.

244 At Kiel, Franz Schütt (1859–1921) entitled his study –sporulation– of
245 dinoflagellates, although he illustrated the ecdysis more than the formation of spores
246 (Schütt 1887). The stressing conditions of capture and manipulation induce that the
247 thecate cell abandons its theca, swimming temporarily as a naked form that will later
248 regenerate a new theca (Fig. 1F). During the ecdysis, the cell expanded, splitting and
249 shedding the thecal plates, and the naked cell escapes through the open apex or at the
250 cingulum level. The apical pore plate is kind of masonry keystone maintaining the arch
251 formed by the apical plates. In the early steps of the ecdysis, the anterior sutures of the
252 apical pore plates begin to separate, and that resulted in a temporarily bifurcated or pointed
253 apex. Schütt (1887) illustrated the ecdysis of *Peridinium acuminatum*, showing that the
254 apex is pointed after the split of the apical plates prior the release of the naked cell (Fig.
255 1F). This suggests that Ehrenberg's illustrations of *P. acuminatum* may correspond to
256 individuals beginning the ecdysis.

257 On August 1893, Pouchet observed the proliferation of a thecate dinoflagellate in
258 the coast of Brittany, French Atlantic Ocean. This time he illustrated the cell in ventral
259 view, showing a polygonal cell that resembles his *Peridinium polyedricum* from the
260 Mediterranean Sea (Fig. 1G). However, Pouchet identified it as *Peridinium acuminatum*
261 without comments on the similarity with *P. polyedricum* or *Goniodoma acuminatum*.
262 Pouchet (1893) illustrated the ecdysis and posterior evolution of the naked form using the
263 name *Peridinium acuminatum*, similar to the study by Schütt (1887) on the same species
264 at Kiel. Pouchet's research note to the French Academy of Sciences was focused on the

265 morphological changes of the species in a culture, and he omitted the discussion on the
266 identity. Pouchet passed away some months later without providing more information. In
267 the late 19th century, little was known about the nutritional requirements of
268 dinoflagellates, and a culture was just only placing the cells in filtered seawater. As usual,
269 the response of a thecate dinoflagellate to these stressing conditions was to shed the theca
270 (=ecdysis). Pouchet (1893) noted the intraspecific variability, and that these naked cells
271 that escaped from the theca were mistaken for the cells of the truly unarmoured
272 dinoflagellate *Gymnodinium* F.Stein 1878. Pouchet's *Peridinium acuminatum* (Fig. 1G)
273 was *Goniodoma acuminatum* and his own *Peridinium polyedricum* (Fig. 1E). The
274 presence of this species is confirmed in the region. For example, the first molecular data
275 for that species, retrieved as 'Goniodoma polyedricum', is available from Brittany where
276 Pouchet collected his samples ([accession number JQ247712](#)).

277 Eugen Jørgensen (1862–1938) carried out his first plankton studies in the
278 Norwegian coasts, where the publication by Claparède and Lachmann (1859) was a key
279 reference. Jørgensen (1899) proposed the new combination *Glenodinium acuminatum*
280 citing *Peridinium acuminatum* by Ehrenberg, and Claparède and Lachmann 1859, and he
281 added *Glenodinium trochoideum* F.Stein 1883 as heterotypic synonym. Jørgensen (1899,
282 p. 32) provided a short description without illustration, “schlüpft aber nicht wegen ihrer
283 geringen Größe durch das Netz. Das *Peridinium acuminatum* Ehr., kann nach meiner
284 Ansicht nmmoglicb dieselbe Art wie *Goniodoma acuminatum* Stein sein... und die
285 Dimensionen entsprechen sehr wohl dieser Art.”. Jørgensen's observations in Norway fit
286 well with the description and size reported for *Peridinium acuminatum* sensu Claparède
287 and Lachmann 1859 at Bergen fjord. Jørgensen observed a bloom of the common small
288 cells that Claparède and Lachmann misidentified as *Peridinium acuminatum*. A
289 comparison of the original illustrations of *Glenodinium trochoideum* (Fig. 1D) and the
290 basionym *Peridinium acuminatum* (Fig. 1A) evidences that they are unrelated species.
291 However, Jørgensen (1889) merged *Glenodinium trochoideum* and *Peridinium*
292 *acuminatum*. *Glenodinium acuminatum* (Ehrenberg) Jørgensen and *Goniodoma*
293 *acuminatum* (Ehrenberg) F.Stein are nomenclatural synonyms because they share
294 *Peridinium acuminatum* as basionym, but Jørgensen (1899) did not list *Goniodoma*
295 *acuminatum* as synonym of *Glenodinium acuminatum*. Jørgensen (1899) considered that
296 *Goniodoma acuminatum* and *Peridinium polyedricum* are synonyms, and distinct from
297 *Peridinium acuminatum*. Jørgensen (1899, p. 33) reported, “Der Name *Goniodoma*

298 *acuminatum*, der übrigens sehr schlecht passt, wird mit *G. polyedricum* (Pouch.)
299 umgetauscht werden können, indem *Peridinium polyedricum* Pouch. identisch”.
300 Jørgensen was based on the misidentification of *Peridinium acuminatum* by Claparède
301 and Lachmann (1859). The synonymy of the medium-sized angled cells of *Peridinium*
302 *acuminatum* and the small ovoid cells of *Glenodinium trochoideum* was unfortunate, and
303 Jørgensen’s new combination *Goniodoma polyedricum* was unnecessary.

304 Pavillard (1915) used the name *Goniodoma acuminatum*, and considered
305 *Peridinium polyedricum* Pouchet as a junior synonym. Pavillard reported, “Jørgensen
306 (1899) a proposé une rectification systématique tendant à substituer au binôme établi par
307 Stein le nom de *G. polyedricum* (Pouchet). Cette innovation n’a pas été généralement
308 adoptée”. However, Jørgensen’s interpretation was partially followed in popular
309 monographs from northern Europe (Paulsen 1908, Schiller 1935). Schiller (1935, p. 137)
310 reported the small ovoid taxon as *Peridinium trochoideum* (F.Stein) Lemmermann, and
311 he listed as synonym *Glenodinium acuminatum* (Ehrenberg) Jørgensen 1899 and the
312 basionym *Glenodinium trochoideum* F.Stein. Under the current nomenclatural practices,
313 Schiller (1935) should use the epithet ‘*acuminatum*’ instead of ‘*trochoideum*’. Paulsen
314 (1908) or Schiller (1935) listed as synonym ‘*vix Peridinium acuminatum* Ehrenberg’ (*vix*
315 = reluctantly, with difficulty). It is certainly difficult to find a relationship between
316 *Peridinium acuminatum* Ehrenberg and *Glenodinium trochoideum* F.Stein.

317

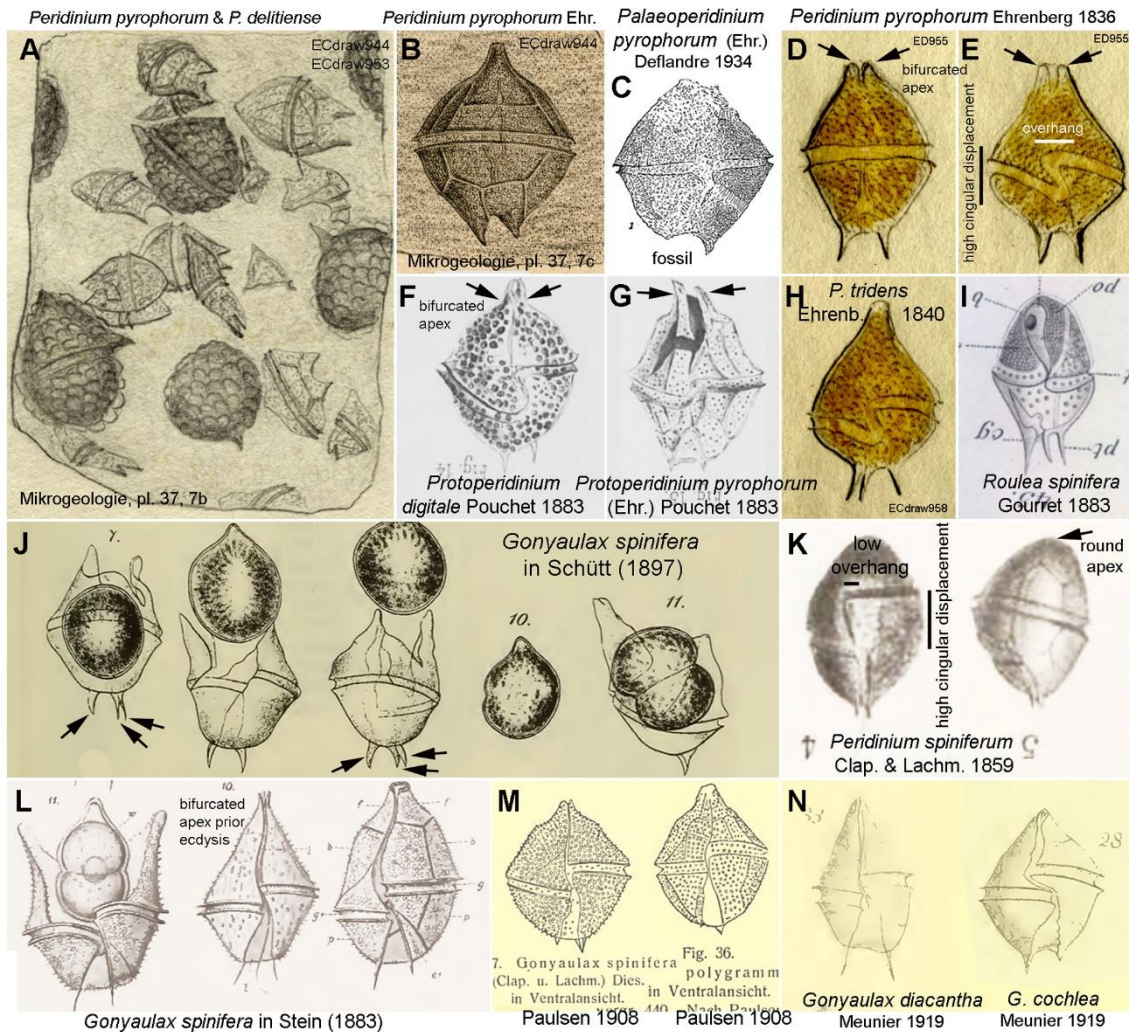
318 **3.4. Ehrenberg’s style illustrating dinoflagellates**

319 **3.4.1. Species of *Gonyaulax***

320 The analyses of the style of Ehrenberg’s drawings are useful to interpret the identity of
321 the taxa. The reader has to take into account that the authors in the 19th century often
322 illustrated morphological structures that do not exist. For example, until 1884, all the
323 authors illustrated a crown of cilia around the cingulum of the dinokont dinoflagellates,
324 while they were really observing the characteristic ribbon-like transversal flagellum. An
325 anomaly in Ehrenberg’s drawings of *Peridinium acuminatum* is the excessively pointed
326 apex (Fig. 1A) when compared to the more common morphology in this taxon (Fig. 1B).
327 This pointed triangular apex is always missing in *Glenodinium trochoideum* (Fig. 1D).
328 Was Ehrenberg exaggerating the pointed shape of the apex of *Peridinium acuminatum*?
329 Probably Ehrenberg observed individuals at the beginning of the ecdysis as illustrated by

330 Schütt (1887) at Kiel (Fig. 1F). For example, Ehrenberg also illustrated his *Peridinium*
331 *pyrophorum* with a bifurcated apex evidencing that the cell was beginning the ecdysis
332 (ECdraw955).

333 Among the marine dinoflagellates, Ehrenberg cited the name *Peridinium*
334 *pyrophorum* Ehrenberg (1838, pl. 1, figs. 1, 4 ex Wetzel 1933, p. 164–165; 1854, legend
335 pl. 37), and the illustrations are available in ECdraw944, 953 and 955, and published at
336 <https://www.biodiversitylibrary.org/item/207209#page/211/mode/1up> . A first problem
337 is that the illustration of *Peridinium pyrophorum* from sediments (fossil material) seems
338 to correspond to a species of the current extant genus *Protoperidinium* Bergh 1881 (Fig.
339 2A–B), while the illustration of the live material of *Peridinium pyrophorum* from Kiel
340 unequivocally corresponded to a species of the genus *Gonyaulax* Diesing 1866. Later,
341 Deflandre (1934) proposed *Palaeoperidinium* cf. *pyrophorum* for the fossil *Peridinium*
342 *pyrophorum* (Fig. 2C). It should be noted that the fossilized form of *Gonyaulax* is a cyst
343 with spines as illustrated in ECdraw954. The live cell that Ehrenberg labelled as
344 *Peridinium pyrophorum* (ECdraw955) is photosynthetic (yellow cytoplasm with
345 brownish corpuscles that may represent the chloroplasts). The ventral view showed the
346 two ends of the cingulum at distinct heights (high cingular displacement of about three
347 cingular widths) and with overhang of the ends of the cingulum (Fig. 2D–E). This is the
348 distinctive Z-shaped junction of the cingulum and sulcus as commonly represented in the
349 literature for the type species of the genus *Gonyaulax*, *G. spinifera* (Claparède &
350 J.Lachmann 1859) Diesing 1866 *auct. mult.* The illustration of *Peridinium pyrophorum*
351 (ECdraw955) showed a conical epitheca tapering into a bifurcated apex, and a trapezoidal
352 hypotheca with two prominent antapical spines. Ehrenberg observed the beginning of the
353 ecdysis, and he interpreted the split of the apical plates as a bifurcated apex (Fig. 2E).
354 Ehrenberg also illustrated two posterior spines, which were thicker than those usually
355 present in the species of *Gonyaulax*. This suggests that Ehrenberg represented a realist
356 general cell shape, but he exaggerated the body extensions (Fig. 2D–E).



357

358 **Fig. 2.** Line drawings of species of *Gonyaulax* and *Protoperidinium*.

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The illustrations of *Peridinium pyrophorum* (ECdraw955) are sufficient for the species identification, but they were never published (Fig. 2D–E). Unequivocally, Ehrenberg’s *Peridinium pyrophorum* is the first illustration of the genus *Gonyaulax* Diesing 1866, but that species was never transferred into that genus. Pouchet (1883) described *Protoperidinium digitale* with the distinctive Z-shaped junction of the cingulum and sulcus (high circular displacement and overhang). Pouchet also illustrated the bifurcated apex, and more realistic dimensions of the antapical spines (Fig. 2F). Ehrenberg exaggerated the thickness of the spines when describing *Peridinium pyrophorum*. Unequivocally *Protoperidinium digitale* C.H.G.Pouchet 1883, currently *Gonyaulax digitalis* (C.H.G.Pouchet) Kofoid 1911, is a junior synonym of *Peridinium pyrophorum* Ehrenberg. On the other hand, Pouchet (1883) illustrated *Peridinium pyrophorum* as a cell with low circular displacement without overhang, and short antapical spines (Fig. 2G). Pouchet (1883) proposed the new combination

373 *Protoperidinium pyrophorum* (Ehrenberg) C.H.G.Pouchet 1883, but his illustration is not
374 conspecific with *Peridinium pyrophorum*. The illustration [ECdraw955](#) exaggerated the
375 dimensions of the antapical spines. The bifurcated apex was indicating that the cell began
376 the ecdysis (Fig. 2E). This is the usual response of cells of many gonyaulacoid
377 dinoflagellates (i.e., *Peridinium acuminatum*) to the stress of capture and manipulation
378 (Fig. 1F).

379 Ehrenberg (1840) described *Peridinium tridens* also at Kiel ([ECdraw958](#)).
380 Ehrenberg probably observed the typical individuals with two antapical spines that he
381 pooled as *Peridinium pyrophorum*. Ehrenberg paid attention on the less common
382 individuals with three antapical spines (Fig. 2H). He used this feature to propose
383 *Peridinium tridens* (=with three teeth). There are two options: *Peridinium tridens* (Fig.
384 2H) corresponded to individuals of *Peridinium pyrophorum* (Fig. 2E) that developed
385 three antapical spines, or certainly *Peridinium tridens* is a distinct species. We have to
386 neglect the value of the number of antapical spines because this is not a stable diagnostic
387 character in the genus *Gonyaulax*. The species has typically two antapical spines, but
388 individuals with three spines can be also found in the same population. This species
389 cannot be confused with *Amylax* (= *Gonyaulax triacantha*), a species with three posterior
390 spines, but very distinct shape. Ehrenberg's illustration of *Peridinium tridens* showed a
391 cell with a more elongated epitheca, and less cingular displacement and overhang of the
392 cingulum ends in comparison to *Peridinium pyrophorum*. This suggests that *Peridinium*
393 *tridens* is a distinct species. *Peridinium tridens* is probably an earlier description of
394 *Gonyaulax spinifera* (Claparède and Lachmann 1859) Diesing 1866 *auct. mult.*

395 Gourret (1883) also described a species of *Gonyaulax* as *Roulea spinifera* with three
396 antapical spines (Fig. 2I). Stein (1883) did not report *P. pyrophorum*. He illustrated cells
397 identified as *Gonyaulax spinifera* from Kiel, but distinct from the illustration of the
398 basonym, *Peridinium spiniferum* Claparède & J.Lachmann 1859 (Fig. 2K). One of the
399 illustrations of *Gonyaulax spinifera* sensu Stein (Fig. 2L) corresponded to the species
400 later described as *Gonyaulax diacantha* Meunier 1919 from the North Sea (Fig. 2N). Stein
401 (1883) also provided other illustration that corresponded to other distinct species (Fig.
402 2L). At Kiel, Schütt (1887) illustrated the phenomenon of the ecdysis for a species
403 identified as *Gonyaulax spinifera*. Schütt showed the cells with the shape of *Peridinium*
404 *tridens*, including individuals with two or three antapical spines (Fig. 2J). This suggests
405 that Ehrenberg's *Peridinium tridens* is an earlier description of the species that further

406 authors have identified as *Gonyaulax spinifera* (Claparède et J.Lachmann 1859) Diesing
407 1866 *auct. mult.*

408 The most commonly reported species of *Gonyaulax* is *Gonyaulax spinifera*, the
409 type of the genus and family. It is also type of the order Gonyaulacales F.J.R.Taylor 1980,
410 although we can use the order Pyrocystales Haeckel 1894/Apstein 1909 (ICN,
411 Recommendation 16A). We can expect that the identity of an important species is clear.
412 However, there are doubts about its identity. In the molecular phylogenies, we can find
413 at least four distinct clades for sequences identified as *Gonyaulax spinifera*. Claparède
414 and Lachmann (1859) illustrated *Peridinium spiniferum* as an ellipsoidal cell, with a
415 round apex, high cingular displacement (about five cingular widths), and very slight
416 overhang. In the left ventral view, the hypotheca extended for 2/3 of the total cell length
417 (Fig. 2K). *Peridinium spiniferum* is the basionym of *Gonyaulax spinifera*. However,
418 *Gonyaulax spinifera* is commonly represented as cell with a conical epitheca, tapering
419 into a truncate apex, with a slightly pre-median cingulum. The hypotheca is polygonal,
420 like an isosceles trapezoid (Fig. 2M). It is difficult to assume the conspecificity of
421 *Peridinium spiniferum* and *Gonyaulax spinifera auct. mult.* The illustrations of
422 *Gonyaulax spinifera* in further literature (Fig. 2M) fit better with *Peridinium tridens*
423 (excluding the anecdote of the three antapical spines) (Fig. 2H). Authors will submit
424 proposals on the case of *Gonyaulax spinifera*. This has an easy solution if we admit that
425 *Peridinium pyrophorum* is validly published with a descriptive statement (ICN, art. 38.4),
426 then:

427 *Gonyaulax pyrophorum* (Ehrenberg) *comb. inedit.*

428 Basionym: *Peridinium pyrophorum* Ehrenberg 1836, *Ber. K. Akad. Wiss. Berlin* 1836:
429 114.

430 Heterotypic synonym: *Gonyaulax digitalis* (C.H.G.Pouchet 1883) Kofoid 1911

431

432 *Gonyaulax tridens* (Ehrenberg) *comb. inedit.*

433 Basionym: *Peridinium tridens* Ehrenberg 1836, *Ber. K. Akad. Wiss. Berlin* 1836: 201.

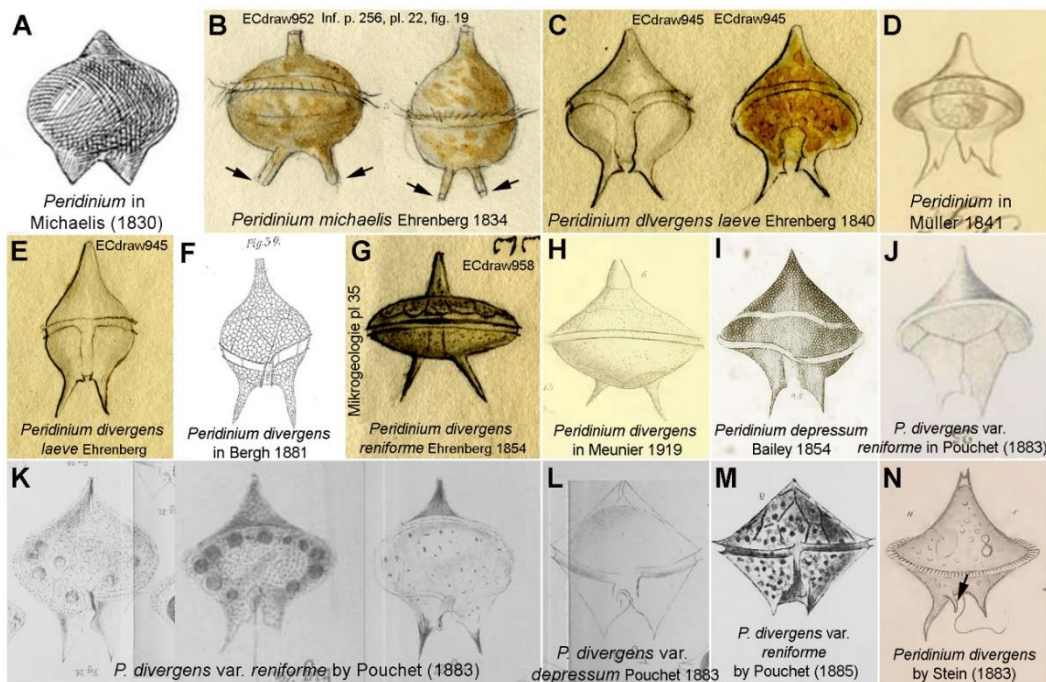
434 Homotypic synonym: *Ceratophorus tridens* (Ehrenberg) Diesing 1850

435 Heterotypic synonym: *Gonyaulax spinifera* (Claparède & J.Lachmann 1859) Diesing
436 1866 *auct. mult.*

437

438 **3.4.2. Species of *Protoperidinium***

439 In addition to species of *Gonyaulax*, Ehrenberg described taxa currently classified in the
 440 genus *Protoperidinium* Bergh 1881. Michaelis (1830) paid attention on the phenomenon
 441 of the bioluminescence at Kiel. He illustrated several species of dinoflagellates (*Tripod*
 442 *muelleri*, *Tripod fusus* and *Prorocentrum micans*). It is questionable that these species
 443 were the real responsible because they are not associated or they have too weak
 444 bioluminescence. Michaelis (1830) provided a sketchy illustration of a cell of the genus
 445 *Protoperidinium* Bergh 1881 that could be *Protoperidinium depressum* or *P. divergens*
 446 (Fig. 3A). From samples collected at Kiel, Ehrenberg (1834) proposed *Peridinium*
 447 *michaelis* (Fig. 3B) that could correspond to *Protoperidinium divergens* (Ehrenberg
 448 1841) Balech 1974. However, Ehrenberg's illustrations were unrealistic (ECdraw952).
 449 The apex was truncate, a feature that can find in some species of *Protoperidinium* (not in
 450 *P. divergens*), and the ends of the two antapical horns were truncated, a feature unknown
 451 in *Protoperidinium* (Fig. 3B). Again, Ehrenberg is not realist in the illustration of the
 452 body extensions. The species of *Protoperidinium* are heterotrophic, with the exception of
 453 one tropical species with photosynthetic symbionts (Gómez 2020). The food vacuoles
 454 cannot be confused with chloroplasts because the digestion of *Protoperidinium* is
 455 extracellular. Sporadically some individuals may present red carotenoid granules. Despite
 456 *Protoperidinium* cells are hyaline, Ehrenberg illustrated the cells with brown corpuscles
 457 that could be interpreted as chloroplasts (Fig. 3B).



458
 459 **Fig. 3.** Illustrations of species of *Protoperidinium*.

460 Later, Ehrenberg (1840b) reported more realistic illustrations with the description
461 of *Peridinium divergens*, although not free of discussion. Ehrenberg illustrated the ventral
462 view of a cell missing pigmentation, and the dorsal view with yellowish pigmentation,
463 and brownish irregular corpuscles like chloroplasts (Fig. 3C). Müller (1841) illustrated
464 the same species as *Peridinium* (Fig. 3D). Ehrenberg reported other illustration with a
465 more anterior-posterior elongated cell that corresponded to a distinct species
466 (ECdraw945) (Fig. 3E–F). Ehrenberg (1854) as *Peridinium divergens reniforme*
467 illustrated a cell with a very transversally elongated body, and two long and acute
468 divergent horns (ECdraw958) (Fig. 3G). It is uncertain the identity of this taxon. It could
469 correspond to an unfortunate illustration of *Protoperidinium divergens* (Fig. 3H). In the
470 other side of the Atlantic Ocean, Bailey (1854) carried out a pioneer study of the marine
471 dinoflagellates in America. Bailey described *Peridinium depressum* as a cell with a
472 conical epitheca, and the antapical horn were parallel (not divergent) (Fig. 3I). In the late
473 19th century, the identity of *Peridinium divergens* was associated with considerable
474 confusion. Pouchet (1883) illustrated several distinct species as *Peridinium divergens*
475 (Fig. 3J–K, M). *Peridinium divergens* var. *reniforme* by Pouchet (1883) (Fig. 3K) is even
476 a distinct species in Pouchet (1885) (Fig. 3M). Pouchet proposed the *P. divergens* var.
477 *depressum* that sounds like a fusion the *Peridinium divergens* and *P. depressum*, but his
478 illustration (Fig. 3L) corresponded to a distinct taxon unrelated to these two species. Stein
479 (1883) illustrated, at least, four distinct species as *P. divergens*, including an aberrant
480 form with a third short posterior horn (Fig. 3N). *Peridinium depressum* is a large cell with
481 oblique cingular plane, and consequently the cell settles showing preferentially the apical
482 or antapical views. Although Bailey (1854) illustrated it with parallel antapical horn, this
483 species may also showed divergent antapical horns (Fig. 3I). The size and the plane of
484 the cingulum of *P. depressum* is the main difference with *P. divergens*. The illustration
485 in Michaelis (1830) was probably an earlier description of *P. divergens* or *P. depressum*.
486 Ehrenberg (1834)'s illustration of *Peridinium michaelis* was probably an unfortunate
487 earlier illustration of *P. depressum*. However, the consideration of *Protoperidinium*
488 *michaelis* (Ehrenberg 1834) Bergh 1881 as a senior synonym of *P. depressum* (Bailey
489 1854) Balech 1974 (Fig. 3I) is too risky based on unrealistic structures such as the
490 truncated antapical horns in Ehrenberg's illustration (Fig. 3B).

491 The comparisons of the drawings' style in the decade of 1830 (coinciding with the
492 description of *Peridinium acuminatum*) suggest that Ehrenberg tried to remark the
493 distinctive characters emphasizing the body extensions (i.e., a pointed apex for

494 *Peridinium acuminatum*). Ehrenberg seems to illustrate with realism the body shape, and
495 he illustrated the epitheca and hypotheca of *Peridinium acuminatum* with an angled
496 contour, and the transversal section with polygonal contour. These features are lacking in
497 *Glenodinium (Scrippsiella) trochoideum*. The detail of the cell morphology observed with
498 the optical resolution of earlier microscopes suggest that *Peridinium acuminatum* is larger
499 than *Glenodinium (Scrippsiella) trochoideum*. For these reasons, it is very plausible and
500 that Stein's *Goniodoma acuminatum* certainly corresponded to the taxon that Ehrenberg's
501 described at the same location. Nearly all authors have maintained *Glenodinium*
502 (*Scrippsiella*) *trochoideum* as independent species of *Goniodoma (=Peridinium)*
503 *acuminatum*. In order to avoid to enter in the discussion on the use of *Goniodoma*
504 (*=Peridinium*) *acuminatum*, further authors have used the name *Goniodoma*
505 *polyedricum*. Then, authors were partially following Jørgensen (1899) when using
506 *Goniodoma polyedricum*, but rejecting the synonymy of *Glenodinium (Scrippsiella)*
507 *trochoideum* and *Goniodoma (=Peridinium) acuminatum*.

508

509 **3.5. Recent discussions on *Peridinium acuminatum***

510 Dodge (1981) reviewed the controversy on *Peridinium acuminatum* and he proposed the
511 new genus name *Triadinium* J.D.Dodge under the rules of Botanical Nomenclature.
512 Dodge (1981, p. 279) reported as type species *Triadinium polyedricum* (C.H.G.Pouchet)
513 J.D.Dodge, but citing *Peridinium acuminatum* Ehrenberg as synonym of the basionym.
514 The ICN defines basionym as, “The legitimate, previously published name on which a
515 new combination or name at new rank is based. The basionym does not itself have a
516 basionym”. If *Peridinium acuminatum* Ehrenberg 1834 is a synonym of *Triadinium*
517 *polyedricum* (C.H.G.Pouchet) J.D.Dodge, and *P. acuminatum* Ehrenberg is the basionym
518 on *Goniodoma acuminatum*, then Dodge should propose ‘*Triadinium acuminatum*’.
519 Sournia (1984) in a publication on nomenclature of dinoflagellates deal on the topic
520 ‘*Goniodoma* F.Stein, *Heteraulacus* Diesing, *Triadinium* Dodge 1981’. Sournia rejected
521 the use of *Heteraulacus* and *Triadinium*. For the controversy on *Goniodoma polyedricum*
522 and *G. acuminatum*, Sournia (1984, p. 349) concluded, “la priorité revient sans conteste
523 à *acuminatum*”.

524 The name *Triadinium* was used in the Zoological Nomenclature for the ciliate
525 *Triadinium* Fiorentini 1890, and zoologists considering that dinoflagellates are
526 ambiregnal (protozoa and algae) such as Özdikmen (2009) proposed to replace
527 *Goniodoma* F.Stein 1883 (non the insect *Goniodoma* Zeller 1849) by the new genus

528 named *Yesevius* Özdikmen 2009 with *Peridinium acuminatum* Ehrenberg as basionym of
529 the type species. Özdikmen (2009) also proposed the family Yeseviidae to replace the
530 Goniodomidae/Goniodomataceae and Triadiniaceae. Nakada (2010) proposed the new
531 name *Pyrrhotriadinium* Nakada for *Triadinium* J.D.Dodge. At least, Nakada did not add
532 a new family reporting, “Note that a substitute name for Triadiniidae Dodge (or
533 Goniodomidae) is currently unnecessary, because this taxon may be classified in a family
534 with available name (e.g. Pyrophacidae = Pyrophacaceae, Ostreopsidae =
535 Ostreopsidaceae)”. However, the molecular data reveal that the genus of *Peridinium*
536 *acuminatum* Ehrenberg 1834 (retrieved as *Goniodoma polyedricum*) is not closely related
537 to *Pyrophacus* or *Ostreopsis*, unless we consider a macro-family in the
538 Pyrocystales/Gonyaulacales (Gómez 2020). The basionym of the generitype of
539 *Pyrrhotriadinium* is *Peridinium polyedricum* C.H.G.Pouchet, that is a junior synonym of
540 the generitype of *Goniodoma* F.Stein, *G. acuminatum* (Ehrenberg) F.Stein. Then, we
541 should use *Goniodoma acuminatum* for the gonyaulacoid dinoflagellate that Ehrenberg
542 described as *Peridinium acuminatum*. However, authors avoid to enter in the discussion
543 when using *Goniodoma polyedricum*. The only nomenclatural problem is what to do with
544 *Heteraulacus* Diesing 1850 or *Heteroaulax* Diesing 1866, solving whether these genera
545 names are valid, and they share the same type of *Goniodoma* F.Stein 1883. The NCA
546 accepted the practice of selection of the type species by Loeblich and Loeblich (1966)
547 (see Report of the Nomenclature Committee for Algae 22, Andersen 2020). Then, it only
548 remains to know whether *Heteraulacus* and/or *Heteroaulax* Diesing 1866 are valid
549 names.

550

551 **3.6. Problem creation**

552 Gottschling and Elbrächter in Kretschmann et al. (2015) resuscitated the error by
553 Claparède and Lachmann (1859), and Jørgensen (1899). They proposed that *Peridinium*
554 *acuminatum* Ehrenberg 1836 is a senior synonym of *Scrippsiella trochoidea* (F.Stein
555 1883) Loeblich 1976. Kretschmann et al. considered that *Peridinium acuminatum*
556 Ehrenberg is a peridinioid dinoflagellate instead of a gonyaulacoid dinoflagellate,
557 *Goniodoma* F.Stein 1883, contrary to the *status quo* in the literature. They proposed the
558 new combination *Scrippsiella acuminata* (Ehrenberg) Kretschmann, Elbrächter,
559 Zinssmeister, S.Soehner, Kirsch, Kusber & Gottschling 2015. This is authored by W.-H
560 Kusber, co-author of the last edition of the ICN (Turland et al. 2018) and member of the

561 NCA that vote the proposals. A proposal can be well-written using the nomenclatural
562 terminology, but based on a wrong taxonomical interpretation. Even if we accept the very
563 questionable synonymy of *Goniodoma acuminatum* (\equiv *Peridinium acuminatum*) (Fig.
564 1A–B) and *Scrippsiella trochoidea* (\equiv *Glenodinium trochoideum*) (Fig. 1D), the molecular
565 phylogenies reveal that generitype of *Scrippsiella* Balech 1959 is closely related to the
566 generitype *Duboscquodinium* Grassé 1952, and *Scrippsiella acuminata* should be placed
567 in *Duboscquodinium* (Coats et al. 2010). Contrary to the principle of priority,
568 Kretschmann et al. (2015) transferred the generitype of *Goniodoma* F.Stein 1883 into
569 *Scrippsiella* Balech 1959. These authors, Gottschling and Elbrächter (2015), submitted
570 the proposal (2382) to conserve the name *Scrippsiella* against *Heteraulacus* and
571 *Goniodoma*. The proposal was recommended (Report of the Nomenclature Committee
572 for Algae 15, Prud’homme van Reine 2017). Consequently, a second proposal (2383) to
573 reject the derived family name Goniodomataceae (Elbrächter and Gottschling 2015) was
574 also recommended (Prud’homme van Reine 2017). The family name Heteraulacaceae
575 Loeblich & Drugg 1968 was also proposed for *Heteraulacus*. The recommendation of the
576 proposals (2382–2383) have an additional problem because the name Goniodomataceae
577 is suitable name for the clade of the genera *Goniodoma*, *Psammodinium*, *Fukuyoa* and
578 *Gambierdiscus* that are distantly related to the genera *Ostreopsis* and *Pyrophacus*, types
579 of the families Ostreopsidaceae and Pyrophacaceae, respectively (Gómez 2020). The
580 NCA rejected the Goniodomataceae without providing an alternative name, maybe
581 *Pyrrhotriadinium*, for the gonyaulacoid dinoflagellates currently classified in that family.
582 The name *Scrippsiella trochoidea* of common use in the literature is now replaced by a
583 new name. This is not an example of the ‘nomenclatural stability’ claimed by Elbrächter
584 and Gottschling in their proposals. *Peridinium acuminatum* Ehrenberg is the species that
585 Stein (1883) illustrated as *Goniodoma acuminatum* (Fig. 1A–B). Even, if we accept the
586 questionable synonymy of *Peridinium acuminatum* (Fig. 1A) and *Glenodinium*
587 *trochoideum* (Fig. 1D), the designation of an illustration of *Goniodoma acuminatum*
588 sensu Stein 1883 (Fig. 1B) as type of the genus *Goniodoma* avoids the problems.

589

590 **4. The case of *Amphidoma***

591 (2577) Proposal to conserve the name *Amphidoma* (Dinophyceae) as being of feminine
592 gender and with a conserved type. Tillmann, U., Gottschling, M. 2018. *Taxon* 67: 203–
593 203. No recommended (Andersen 2020).

594

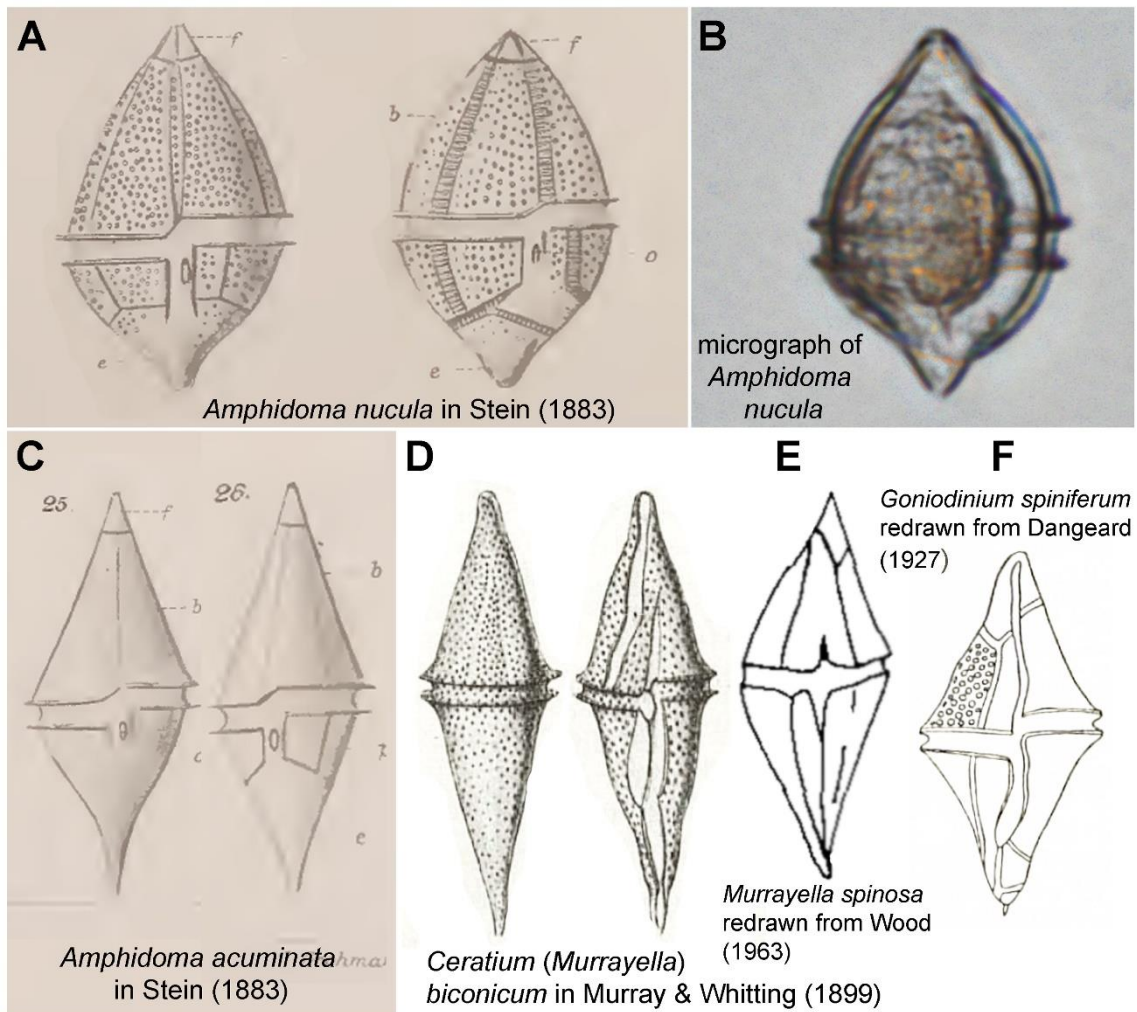
595 Stein (1883) proposed *Goniodoma* with *G. acuminatum* as type species. The
596 ending of the epithet indicates that the genus is neuter. The etymology is Greek γωνία
597 (gōnía), corner, angle: Latin *genu*, *genus*, knee; gender neuter. Stein (1883) also proposed
598 the genus *Amphidoma*, with two species *A. nucula* and *A. acuminata*. The species epithet
599 *nucula* (small nut) cannot be declined as ‘nuculum’, but for the second species Stein had
600 the option to use *acuminat-us/a/um*, and he established the genus as feminine. The genus
601 is neuter based on the etymology: Greek ἀμφί (amphí) “on both sides”; gender neuter,
602 Ancient Greek δῶμα (dōma), Latin *doma*, *domatis*, dwelling, house; gender neuter.
603 Sournia (1984, p. 84) reported that *Amphidoma* is neuter, and then the type is *Amphidoma*
604 ‘*acuminatum*’. The ICN article 62.1 states, “A generic name retains the gender assigned
605 by nomenclatural tradition, irrespective of classical usage or the author’s original usage”.
606 What is the nomenclatural tradition? The genera ending in *-doma*, more commonly used
607 in the zoological nomenclature, is usually treated as feminine. The proposal (2577) to
608 conserve the *Amphidoma* as being of feminine gender was not recommended. The NCA
609 concluded, “there is no need to assign a gender by conservation” (Report of the
610 Nomenclature Committee for Algae 22, Andersen 2020). This part of the proposal is just
611 only a diversion.

612 The second part (2577) proposed to conserve *Amphidoma* with a conserved type.
613 This part is more interesting because the designation of one or other type have important
614 consequences. Tillmann and Gottschling (2018) did not explain the motivation of the
615 proposal. The genus *Amphidoma* have traditionally received low attention because it was
616 predominantly found in the warm open ocean, far from the specialized laboratories.
617 Tillmann et al. (2009) described the genus *Azadinium* for tiny species that were previously
618 overlooked for other taxa. *Azadinium* is toxigenic, and since then numerous new species
619 have been described. The molecular phylogenies showed that the DNA sequences of the
620 species *Amphidoma caudata* Halldal clustered closely related to the sequences of the
621 genus *Azadinium*. Tillmann and others classified *Azadinium* in the Amphidomataceae
622 Sournia 1984. In addition, Tillmann described other species belonging to *Amphidoma* (*A.*
623 *alata* Tillmann, *A. cyclops* Tillmann, *A. languida* Tillmann, R. Salas & Elbrächter, *A.*
624 *parvula* U. Tillmann & Gottschling, *A. trioculata* Tillmann). *Amphidoma caudata* is not
625 the type species, then it is not confirmed that these recent new species belong to
626 *Amphidoma*, and that *Azadinium* can be classified in the Amphidomataceae.

627 A genus is defined by its type species. Stein (1883) illustrated two species:
628 *Amphidoma nucula* and *A. acuminata*. In the text, Stein (1883, p. 20) reported,
629 “*Amphidoma* mit der allein sicheren Art *Amph. nucula* (Taf. IV, Fig. 21–24)” (~with the
630 only species *Amphidoma nucula*). In the figure legend of the plate 4, Stein reported the
631 figures 21–24 of *Amphidoma nucula*, and the figures 25–26 of *Amphidoma acuminata*.
632 Stein (1883) provided more figures and with more detail of *Amphidoma nucula*. Loeblich
633 and Loeblich (1966, p. 16) reported, “*Amphidoma* Stein, 1883, p. 9, 20. Type species: *A.*
634 *acuminata* Stein, 1883, pl. 4, fig. 25, 26; fixed by SD Loeblich Jr. & Loeblich III, herein”.
635 Loeblich and Loeblich (1966) did not explain why they contradicted Stein (1883) who
636 only cited *Amphidoma nucula* as the single species of the genus. Silva (1979) and in this
637 card note of *Amphidoma* at *Index Nominum Algarum (INA)*,
638 <https://ucjeps.berkeley.edu/cgi-bin/porp.cgi.pl?500412> reported, “*A. nucula* only species
639 cited by Stein. LT. *A. acuminata*, Loeblich Jr. & III 1966; 16. **incorrect!**”. Sournia (1984,
640 p. 346) in a publication on nomenclature of dinoflagellates reported, “A noter que
641 l’espèce-type du genre est *A. nucula* Stein comme l’indique implicitement Stein (1883, p.
642 20) et comme le rappelle Silva (1979), et non *A. acuminatum* Stein comme l’écrivent
643 Loeblich et Loeblich (1966)”. Gómez (2012, p. 117) in a dinoflagellate classification
644 reported *Amphidoma nucula* as the type of *Amphidoma* following Silva (1979) and
645 Sournia (1984). Unpublished molecular data of *Amphidoma nucula* reveal that this
646 species is unrelated to the other available sequence of *Amphidoma* spp. and *Azadinium*
647 spp. For that reason, Gómez (2012, 2020) restricted the Amphidomataceae to *Amphidoma*
648 *s.s.*, and placed other species of *Amphidoma* such as *A. caudata* and *Azadinium* spp. in an
649 undescribed family ‘Family of *Amphidoma caudata*’. This implies that *Amphidoma*
650 *caudata*, and other congeneric species recently described by Tillmann should not be
651 placed in *Amphidoma*, and *Azadinium* is not a member of the Amphidomataceae. The
652 NCA reported, “Therefore, with regard to the second component of the proposal, the NCA
653 concluded that *A. acuminata* was a validly published name, that the type was not selected
654 by a mechanical method, and that no evidence was provided showing doubtful congeneric
655 classification. The NCA determined that *A. acuminata* should remain as the type; the
656 proposal is not recommended” (Report of the Nomenclature Committee for Algae 22,
657 Andersen 2020).

658 After confirming *Amphidoma acuminata* as type, the species *Amphidoma nucula*
659 will need to be placed in other genus. Sournia (1984) proposed the family

660 Amphidomataceae citing *A. nucula* as type. Stein (1883) provided four illustrations of
661 *Amphidoma nucula* (Fig. 4A), and it is easily recognizable in oceanic plankton samples
662 (Fig. 4B). There are no major problems in the identification of *Amphidoma nucula*, and
663 this allows to establish which species are circumscribed to *Amphidoma*. In contrast, Stein
664 (1883) provided only two illustrations of *Amphidoma acuminata* showing the same view,
665 and missing details on the tabulation (Fig. 4C). The only information about *A. acuminata*
666 is the figure legend, “Eine noch zweifelhafte Art mit nicht vollständig ausgebildetem
667 Panzer” (zweifelhaft = doubtful; nicht vollständig = incomplete). Stein (1883) admitted
668 that *A. acuminata* is a dubious species with an incomplete theca. Although the illustrations
669 of *A. acuminata* are scarcely detailed, the shape of the cell may correspond to species of
670 the genus *Centrodinium* Kofoid 1907 (Gómez and Artigas 2019) which species were
671 previously placed in the genera *Murrayella* Kofoid 1907, *Pavillardinium* de Toni 1936
672 and *Goniodinium* Dangeard 1927 (Fig. 4D–F). Stein (1883) examined samples from open
673 warm oceans, where species of *Centrodinium* are common. As *Amphidoma acuminata* he
674 probably showed the earliest illustration of *Centrodinium*. The NCA confirmed
675 *Amphidoma acuminata* as type species, then about 16 species of *Centrodinium* can be
676 transferred into *Amphidoma*. The species *Amphidoma caudata*, and the Tillmann’s new
677 species (*A. alata*, *A. cyclops*, *A. languida*, *A. parvula*, *A. trioculata*) should be placed in
678 other genus, and also *Amphidoma nucula* should placed into another distinct genus. Then,
679 *Azadinium* does not belong to the Amphidomataceae, and that family name will be
680 replaced by other family. *Amphidoma nucula* as type is less problematic than *A.*
681 *acuminata*.



682

683 **Fig. 4.** Illustrations of *Amphidoma nucula*, *A. acuminata* and *Centrodinium* spp.

684

685 **5. The case of *Glenodinium foliaceum* and *Heterocapsa triquetra***

686 (2607) Proposal to conserve the name *Heterocapsa* (Dinophyceae) with a conserved type.

687 Gottschling, Tillmann, Kusber, Hoppenrath & Elbrächter 2018. *Taxon* 67: 632–633.

688 Recommended (Andersen 2020).

689

690 **5.1. Antecedents**

691 Ehrenberg (1840) described *Glenodinium triquetrum* from individuals collected at

692 Wismar, near Kiel, Baltic Sea. He illustrated eleven individuals that suggest that the

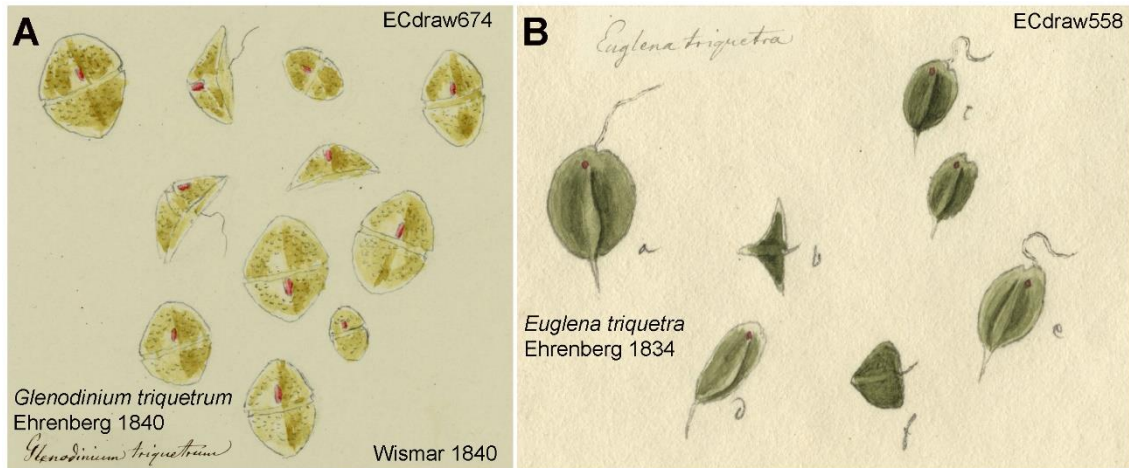
693 species was abundant ([ECdraw674](#)) (Fig. 5A). He showed individuals divided into two

694 size classes and two views: One view showed cells with a more or less ellipsoidal contour.

695 As the sulcus is not illustrated, it is not possible to establish to which view corresponded

696 the ventral/dorsal or lateral sides. Three individuals were illustrated in other view
697 showing a low triangular contour (Fig. 5A). This time Ehrenberg did not illustrate the
698 crown of cilia around the cingulum that appeared in dinoflagellates until 1884, and two
699 cells in that view showed a short flagellum.

700



701

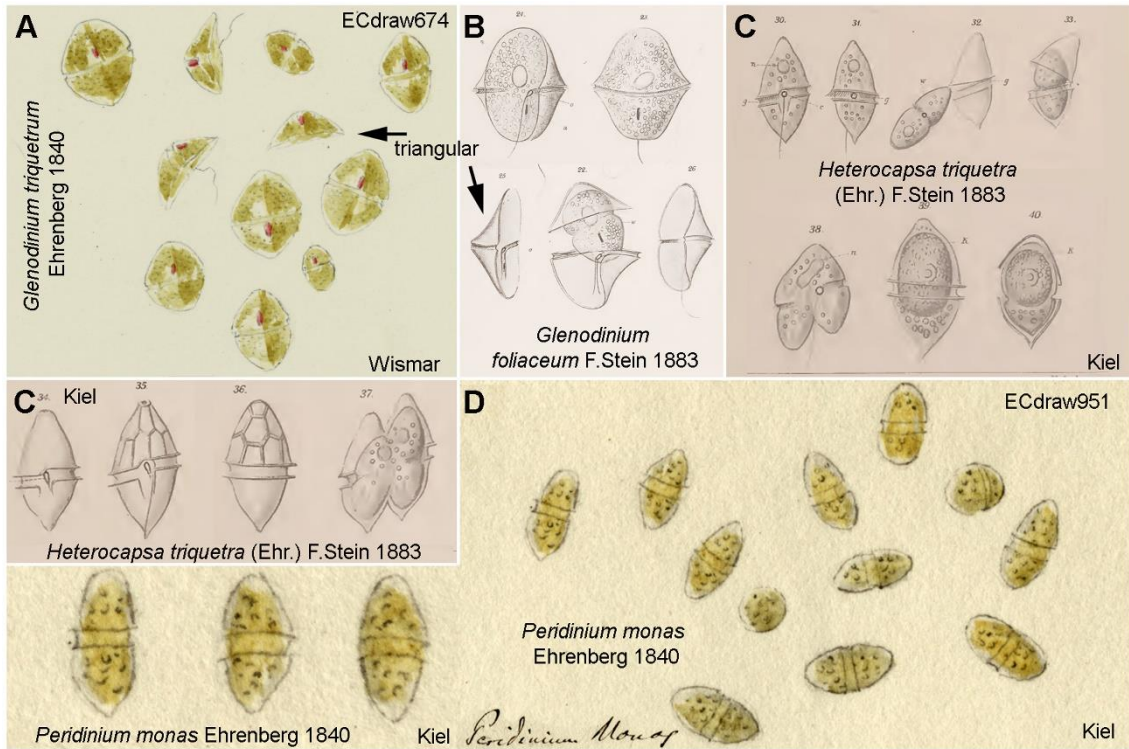
702 **Fig. 5.** Illustrations of *Glenodinium triquetrum* and *Euglena triquetra*.

703

704 The case of *Glenodinium triquetrum* is similar to that of *Euglena triquetra* Ehrenberg
705 (ECdraw558) where he illustrated several individuals, and two of them temporally
706 acquire a triangular contour due to the typical sudden shape changes of the euglenoids
707 (i.e., *Phacus* Dujardin) (Fig. 5B). The etymology of the specific epithet of *Glenodinium*
708 *triquetrum* suggests the typical biconical cell with a triangular contour of the epi- and
709 hypotheca. However, this induces confusion because the cells are ellipsoidal in the most
710 common view under the microscope. Further authors that had not access to the illustration
711 ECdraw674 were expecting to find a cell with triangular shape.

712 From individuals collected at Kiel, Ehrenberg (1840) also described *Peridinium*
713 *monas* Ehrenberg (ECdraw951) (Fig. 6D). He illustrated numerous individuals with an
714 elongated bi-conical contour, with a wide and median cingulum. The apex was blunt and
715 the antapex sometimes pointed (Fig. 6D). The transversal section was circular. Ehrenberg
716 remarked in the short diagnosis that the species was 'sociable'.

717



718

719

Fig. 6. Illustrations of *Heterocapsa triquetra* and *Peridinium monas*.

720

721 5.2. Stein's misinterpretation

722

In 1879, three years after the Ehrenberg's death, Stein (1883) investigated the

723

dinoflagellates at Kiel. It should be noted that the brackish and cold waters of the Baltic

724

Sea are associated with a low dinoflagellate diversity when compared with lower

725

latitudes. Consequently, there are more probabilities that Ehrenberg and Stein observed

726

the same species. Stein was a lumper taxonomist, and he tried to accommodate the

727

identifications to the species already described at that time (mostly the few species

728

described by Ehrenberg, and by Claparède and Lachmann). Ehrenberg never published

729

his illustrations of *Glenodinium triquetrum* that were conserved in the Natural History

730

Museum at Berlin (ECdraw674) (Fig. 6A). Stein did not find the supposed triangular

731

species in agreement with his interpretation of Ehrenberg's diagnosis of *Glenodinium*

732

triquetrum. Stein (1883) described the new species *Glenodinium foliaceum* F.Stein (Fig.

733

6B). The cells were ellipsoidal in the more common view, but sporadically showing a

734

triangular contour only in an uncommon view. Stein's misinterpretation was followed by

735

further authors. Present day, when Ehrenberg's illustrations of *Glenodinium triquetrum*

736

are publicly available (ECdraw674) (Fig. 6A), we can realize that *Glenodinium*

737

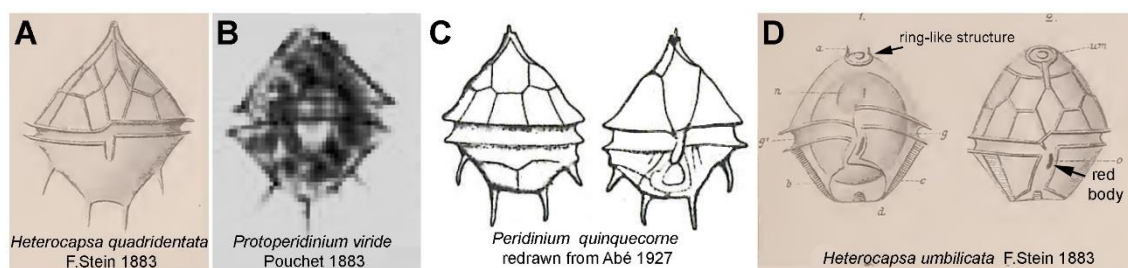
triquetrum and *G. foliaceum* are conspecific. Stein's illustrations identified as

738 *Heterocapsa triquetra* (\equiv *Glenodinium triquetrum*) (Fig. 5C) corresponded to *Peridinium*
739 *monas* Ehrenberg 1840 ([ECdraw951](#)), also described from Kiel with unpublished
740 illustrations (Fig. 6D).

741 Stein (1883, p. 13) placed *Glenodinium triquetrum* and other two new species in
742 the ‘only provisionally’ new genus *Heterocapsa* F.Stein reporting, “Deshalb habe ich aus
743 dem *Glenodinium triquetrum* eine eigene, jedoch nur provisorische Gattung *Heterocapsa*
744 gebildet”. Under the new combination *Heterocapsa triquetra* (Ehrenberg) F.Stein, Stein
745 illustrated individuals that corresponded to *Peridinium monas* Ehrenberg. The presence
746 of a red body in *Glenodinium triquetrum* (\equiv *Glenodinium foliaceum*) is a distinctive
747 character. The members of this family, Kryptoperidiniaceae Lindemann 1928, are named
748 ‘dinotoms’ after hosting a tertiary endosymbiont derived from a diatom, although the
749 symbiont is missing in some members. *Peridinium monas* (\equiv *Heterocapsa triquetra* sensu
750 Stein) may also present a red body
751 (<http://nordicmicroalgae.org/taxon/Heterocapsa%20triquetra>). Ehrenberg (1840)
752 remarked that *Peridinium monas* was a sociable species. This is a fortunate comment
753 because the individuals of *Heterocapsa triquetra* sensu Stein show a remarkable social
754 behaviour, forming groups of individuals that interact and touch among them.

755 Stein (1883) also described other two species: *Heterocapsa umbilicata* F.Stein and
756 *Heterocapsa quadridentata* F.Stein from Samoa and Fiji Islands, respectively. Stein was
757 never in the Pacific Ocean, and he examined preserved material. This implies missing
758 information such as the natural pigmentation or details on the internal organelles. The
759 citations of the type localities as Samoa and Fiji Islands are ambiguous because it is
760 unclear whether Stein refers to the open ocean surrounding the islands, the coastline or
761 the brackish or freshwater bodies on the islands. The open ocean as type locality for
762 *Heterocapsa umbilicata* and *Heterocapsa quadridentata* is discarded because these
763 species are not usually found in the open ocean. They were probably collected in brackish
764 or freshwater environments on the islands. This is a common feature in *Heterocapsa*
765 *triquetra* because its basionym *Glenodinium triquetrum* (\equiv *Glenodinium foliaceum*) is
766 typically found in brackish or estuarine waters (i.e., Baltic Sea). Stein (1883) described
767 with good detail the empty theca of *Heterocapsa quadridentata* (Fig. 7A). Morphological
768 features such as the presence of a red body are missing due to the preservation of the
769 sample after being transported from a tropical island in the central Pacific Ocean into
770 Europe in the 1870’s. Two years later, Pouchet (1885, p. 526) described the same species
771 as *Protoperidinium viridis* C.H.G.Pouchet 1885 (Fig. 7B). He observed live individuals,

772 remarking the green pigmentation and especially the red body, “reconnaissable à sa tache
 773 rouge centrale”. Pouchet’s illustration showed three posterior spines, but this variability
 774 occurred naturally in that species, later described as *Peridinium quinquecorne* var.
 775 *trispiniferum* Aké-Castillo & G.Vázquez. More than 40 year later, *Heterocapsa*
 776 *quadridentata* F.Stein 1883 was re-described as *Peridinium quinquecorne* Abé 1927, also
 777 from the Pacific Ocean (Fig. 7C). Abé (1927, p. 410) described it as, “A small, peculiar
 778 species with four antapical spines on the postmargin”. Abé observed only two complete
 779 individuals that showed four spines, but he used the epithet ‘quinquecorne’ (= five horns).
 780 Abé was a researcher focused on the tabulation of the dinoflagellates, omitting details
 781 such as the pigmentation, red bodies, etc. Abé (1927) only compared his new species with
 782 *Gonyaulax triacantha*, but both taxa are distantly related. Unequivocally, *Heterocapsa*
 783 *quadridentata* F.Stein 1883, *Protoperidinium viride* C.H.G.Pouchet 1885 and *Peridinium*
 784 *quinquecorne* Abé 1927 are conspecific with priority for Stein’s name (Fig. 7A–C).
 785



786

787 **Fig. 7.** Illustrations of *Heterocapsa quadridentata* and *H. umbilicata*.

788

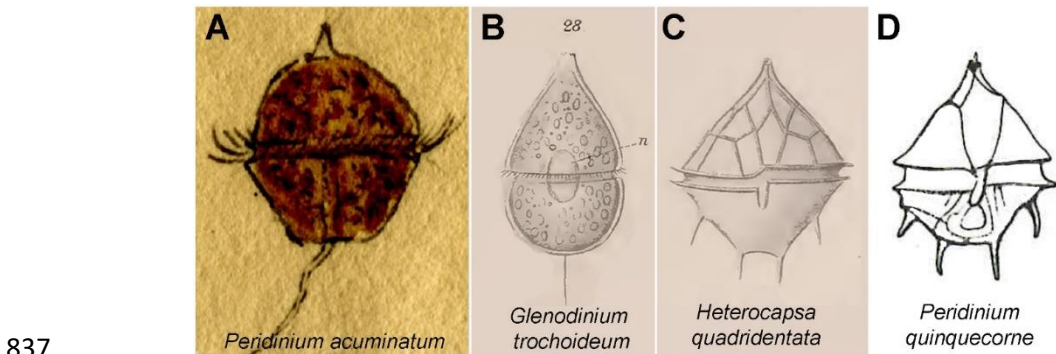
789 Stein (1883) also described *Heterocapsa umbilicata*, a taxon without further
 790 records in the literature. Stein did not show the complete plate arrangement of the
 791 epitheca, and the cell apparently showed a single ring-like apical plate surrounding the
 792 apex that is anomalous (Fig. 7D). These features do not allow to find a similarity with
 793 other species further described. The presence of a red body suggests that *Heterocapsa*
 794 *umbilicata* could be a brackish or freshwater species of the genus *Peridiniopsis*
 795 Lemmermann, which contains species transferred into the Kryptoperidiniaceae. The
 796 basionym of the generitype of the Kryptoperidiniaceae is *Glenodinium foliaceum* F.Stein
 797 1883 (Fig. 6B), a junior synonym of *Glenodinium triquetrum* Ehrenberg 1840 (Fig. 6A)
 798 (\equiv *Heterocapsa triquetra* (Ehrenberg) F.Stein 1883, non *Heterocapsa triquetra* sensu
 799 Stein 1883). Present day, the molecular phylogenies have demonstrated this relationship
 800 for at least for two of the species that Stein (1883) described within the genus

801 *Heterocapsa*. The DNA sequences of *Heterocapsa triquetra* (retrieved from GenBank as
802 *Kryptoperidinium foliaceum*) and *Heterocapsa quadridentata* (retrieved from GenBank
803 as *Peridinium/Blixaea quinquecornis*) are closely related, and these monotypic genera
804 could be merged into a single one. The third species, *Heterocapsa umbilicata* could be
805 also a member of this group, as also it has a red body and the presence of a diatom
806 symbiont. Maybe an accidentally or destined one, but Stein (1883) proposed three species
807 of *Heterocapsa* that certainly belong to the same monophyletic genus within the
808 Kryptoperidiniaceae.

809 In a publication without new observations, Gottschling et al. (2017) transferred
810 *Peridinium quinquecorne*, and five species of *Peridiniopsis* into the new genera *Blixaea*
811 Gottschling and *Unruhadinium* Gottschling, respectively, as members of the
812 Kryptoperidiniaceae. The generic names are in honour of Blixa Bargeld, and the
813 nickname N.U. Unruh of Andrew Chudy, members of the Berlin music group
814 ‘Einstürzende Neubauten’ (‘~collapsing new buildings’). The recommendation 20A.1.h.
815 of the ICN states, “Not dedicate genera to persons quite unconnected with botany,
816 mycology, phycology, or natural science in general”. Numerous dinoflagellate generic
817 names are built using the ending *-dinium-*. When the stem ends in a consonant, a
818 connecting vowel *-i-* or *-o-* is typically added. A genus dedicated to the nickname Unruh
819 is built as *unruh-i-dinium* or *unruh-o-dinium*, not *unruhadinium*. Gottschling et al. (2017,
820 p. 298) reported, “our present choice for new generic names in the dinophytes may
821 stimulate a discussion about the contemporariness and usefulness of Recommendation
822 20A (h) arguing against an unnecessary limitation and for a more liberal and open-
823 minded application of The Code”.

824 Unequivocally, *Heterocapsa quadridentata* F.Stein 1883, *Protoperidinium viride*
825 C.H.G.Pouchet 1885 and *Peridinium quinquecorne* Abé 1927 are conspecific (Fig. 7A–
826 C). Obviously, due to the techniques of fixation in the late 1870’s, the cells of
827 *Heterocapsa quadridentata* transported from Fiji Islands to Europe did not conserve the
828 natural coloration of the internal organelles. Even, if we do not accept the unequivocal
829 synonymy of *Heterocapsa quadridentata* (Fig. 7A) and *Peridinium quinquecorne* (Fig.
830 7B), *Protoperidinium viride* C.H.G.Pouchet 1885 has also the priority over *Peridinium*
831 *quinquecorne* Abé 1927. The choice of *Peridinium quinquecorne* Abé 1927 as type of the
832 genus *Blixaea* Gottschling was unfortunate because it is a junior synonym of *Heterocapsa*
833 *quadridentata* F.Stein 1883. Gottschling et al. (2017) were unable to note that
834 *Heterocapsa quadridentata* and *Peridinium quinquecorne* are conspecific, while these

835 authors consider that *Peridinium acuminatum* and *Glenodinium trochoideum* are
836 synonyms (Fig. 8A–D).



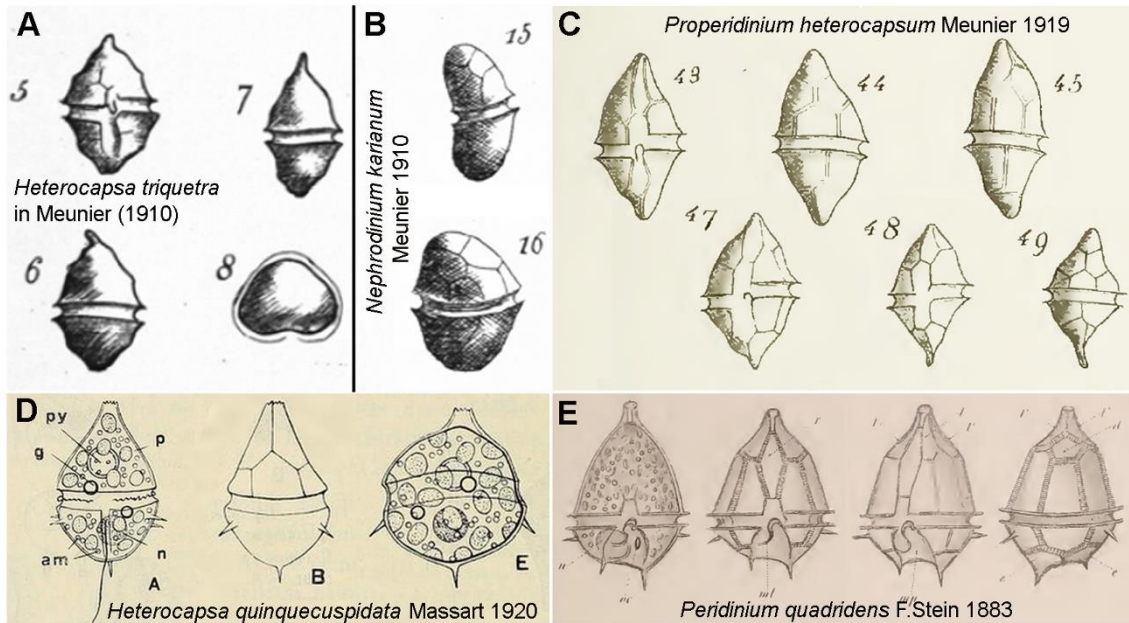
838 **Fig. 8.** Illustrations of *Peridinium acuminatum*, *Glenodinium trochoideum*, *Heterocapsa*
839 *quadridentata* and *Peridinium quinquecorne*.

840

841 **5.3. Other descriptions of *Heterocapsa***

842 From the Arctic Sea, Meunier (1910) reported *Heterocapsa triquetra* with illustrations
843 that corresponded to *Peridinium monas* Ehrenberg (= *Heterocapsa triquetra* sensu Stein)
844 (Fig. 9A). Meunier (1910) also described *Nephradinium karianum* that could correspond
845 to other congeneric species of *Peridinium monas* (Fig. 9B). Later, Meunier (1919)
846 transferred *Heterocapsa triquetra* into the genus *Properidinium* Meunier 1919 as
847 *Properidinium heterocapsum* Meunier 1919 (Fig. 9C). Meunier cited as basionym
848 *Heterocapsa triquetra* sensu Stein (1883), and he did not cite as basionym *Glenodinium*
849 *triquetrum* Ehrenberg. Meunier did not use the epithet ‘triquetrum’, and his aim was to
850 describe a new species based on the Stein’s illustrations, and not a new combination.
851 Erroneously Meunier placed F.Stein as parenthetical authority. Paul C. Silva at [INA](#)
852 reported the species as *Properidinium heterocapsum* Meunier 1919, citing as basionym
853 only *Heterocapsa triquetra* sensu Stein (1883). For sure, Gottschling that claims for a
854 “more liberal and open-minded application of The Code” accepts that *Properidinium*
855 *heterocapsum* Meunier is a new name for *Heterocapsa triquetra* sensu Stein.

856



857

858 **Fig. 9.** Illustrations of *Properidinium heterocapsum* and *Heterocapsa quinquecuspidata*.

859

860 Massart (1920) proposed the new dinoflagellate genus *Heterocapsa* Massart, and
 861 the new species *Heterocapsa quinquecuspidata* Massart from brackish waters also at
 862 Belgium (Fig. 9D). This species is considered a junior synonym of *Peridinium quadridens*
 863 F.Stein 1883 [= *Peridiniopsis quadridens* (F.Stein) Bourrelly] (Fig. 9E), and it is not far
 864 from *Peridiniopsis quinquecuspidata* (Nygaard 1926) Gert Hansen & Flaim 2007. The
 865 main characteristic of the type of the new genus *Heterocapsa* Massart 1920 is the
 866 presence of spines in the hypotheca (Fig. 9D). Gottschling et al. (2017) proposed the new
 867 genus *Unruhadinium* Gottschling within the Kryptoperidiniaceae for species previously
 868 placed in the genus *Peridiniopsis*. Gottschling et al. (2017) reported as diagnostic
 869 character of *Unruhadinium*, “hypotheca with a varying number of more or less distinctive
 870 spines”. The type of the genus *Heterocapsa* Massart 1920 and the type of the genus
 871 *Heterocapsa* F.Stein 1883 are members of the Kryptoperidiniaceae. Fate is capricious, a
 872 genus name and its later isonym are phylogenetically closely related. The generic name
 873 *Heterocapsa* is doubly linked to the Kryptoperidiniaceae.

874 Concerning the suprageneric names associated with *Heterocapsa*, *-capsa-* is a
 875 common stem used for algal names, and *-hetero-* is a common prefix. The suprageneric
 876 names Heterocapsaceae Pascher 1912, Heterocapsales Pascher 1912, Heterocapsales
 877 Fritsch 1927, and Heterocapsae Pascher 1937 are used in the classification of freshwater
 878 microalgae unrelated to dinoflagellates. Is necessary to create more suprageneric names
 879 derived from *Heterocapsa*? Fensome et al. (1993, p. 120–1) proposed the suborder

880 Heterocapsineae Fensome et al. and the family Heterocapsaceae Fensome et al. with the
881 genus *Heterocapsa* F.Stein as type.

882 Balech (1977) examined the tabulation of *Heterocapsa triquetra* sensu Stein 1883.
883 He remarked the difficulties to discern the thin plates, and the variability in the tabulation.
884 For example, the species *Heterocapsa rotundata* (Lohmann 1908) Gert Hansen 1995,
885 common in the Baltic Sea, remained in the unarmoured genus *Amphidinium* until 1995
886 due to the difficulties to observe the thecal plates. Ehrenberg (1840, p. 201) remarked the
887 sociable character in the diagnosis of *Peridinium monas* (= *Heterocapsa triquetra* sensu
888 Stein). These species are easy to culture, and they often appear as contaminants in
889 cultures. Cultured cells of *Heterocapsa* were examined in earlier studies using the
890 electron microscopy. In addition to the variability in the thecal arrangement, this allows
891 observing that some species showed body scales. This is a rare feature in dinoflagellates
892 (i.e., *Amphidinium* Claparède & J.Lachmann). The variable tabulation and the presence
893 or absence of body scales were diagnostic characters used to split *Heterocapsa*, proposing
894 the genus *Cachonina* Loeblich 1968, and two species of *Heterocapsa* were transferred
895 into *Cachonina*. The discussion on the synonymy *Cachonina* and *Heterocapsa* is
896 hereafter summarized. Loeblich (1968) proposed the genus *Cachonina* with *C. niei* as
897 type, and later Morrill (1980) and Morrill and Loeblich (1981) considered that *Cachonina*
898 and *Heterocapsa* were synonyms. The observation of the body scale requires electron
899 microscopy that was not an extended facility in the earlier 1980's. In addition, the
900 variability observed in the plate formula makes difficult using the tabulation as a
901 diagnostic character for the generic split. Dodge (1982) that had access to an electron
902 microscope considered that *Cachonina* and *Heterocapsa* were distinct genera. Dodge
903 (1982, p. 146) proposed the new combination *Cachonina hallii* (Freudental & Lee)
904 J.D.Dodge and he reported it as type species. He listed as synonyms *C. illdefina* Herman
905 & Sweeney 1976, and the type species *Cachonina niei* Loeblich 1968. Other discussion
906 on the synonymy appeared in Sournia (1984, p. 347). Sournia accepted the split into two
907 genera, and transferred *Heterocapsa pygmea* A.R.Loeblich, R.J.Schmidt & Sherley 1981
908 into *Cachonina*. Later, Sournia (1986, p. 93) reported, “provisoirement au moins,
909 maintenir ces genres séparés, contrairement à la position prise par Morrill (1980) et
910 Morrill & Loeblich 1981”. Sournia (1986) reported three species for *Cachonina*, and for
911 *Heterocapsa*, “une seule espece "sure" (*H. triquetra*) et une demi-douzaine d'autres
912 incompletement decrites ou fantomatiques”. The specific epithets ‘pygmea’ or ‘minima’
913 denote the small size, and ‘illdefina’ (= ill define) denotes the difficulties for the

914 identification. There is no support for the generic split because the type species of
915 *Cachonina* and *Peridinium monas* (= *Properidinium heterocapsum*, *Heterocapsa*
916 *triquetra* sensu Stein) cluster together in the molecular phylogenies. After placing the
917 generitype *Heterocapsa triquetra* (= *Glenodinium foliaceum*) in the Kryptoperidiniaceae,
918 the name *Cachonina* is available for *Heterocapsa triquetra* sensu Stein and congeneric
919 species.

920

921 **5.4. Problem creation**

922 The *status quo* on *Heterocapsa* remained until Gottschling, Elbrächter and co-workers
923 split this topic into four papers. In a one paper (Tillmann et al. 2017) proposed
924 *Heterocapsa steinii* Tillmann, Gottschling, Hoppenrath, Kusber & Elbrächter, with an
925 illustration of *Heterocapsa triquetra* in Stein (1883) as type. This is authored again by
926 W.-H. Kusber, co-author of the ICN, and member of the NCA that votes the proposals.
927 In another paper they discussed on the alternative solutions after dismantling the genus
928 *Heterocapsa* (Gottschling et al. 2018a). In another paper, Gottschling et al. (2018b)
929 published the proposal (2607) to conserve the name *Heterocapsa* with a conserved type,
930 *Heterocapsa steinii* Tillmann et al. 2017. In another paper, they proposed
931 *Kryptoperidinium triquetrum* (Ehrenberg) Tillmann, Gottschling, Elbrächter, Kusber &
932 Hoppenrath for *Glenodinium triquetrum*, the basionym of the generitype of *Heterocapsa*
933 F.Stein (Gottschling et al. 2019). In these publications, these authors did not cite that
934 *Heterocapsa steinii* Tillmann et al. 2017 is a homotypic synonym of *Properidinium*
935 *heterocapsum* Meunier 1919, and a heterotypic synonym of *Peridinium monas* Ehrenberg
936 1840.

937 The proposal (2382) on *Peridinium acuminatum* and (2607) on *Heterocapsa*
938 *triquetra* have similar origin because they are based on discrepancies with the
939 interpretations by Stein (1883) of Ehrenberg's taxa. In the case of *Peridinium*
940 *acuminatum*, basionym of the type species of *Goniodoma* F.Stein, Gottschling and
941 Elbrächter proposed to reject the genus *Goniodoma* F.Stein, instead to propose an
942 illustration of *Goniodoma acuminatum* in Stein (1883) as type. In the case of *Glenodinium*
943 *triquetrum*, basionym of the type species of *Heterocapsa*, Gottschling and Elbrächter
944 proposed to conserve the genus *Heterocapsa* F.Stein with a type named *Heterocapsa*
945 *steinii* for one of the illustrations of *Heterocapsa triquetra* in Stein (1883). If someone
946 has doubts on the synonymy of *Peridinium acuminatum* and *Goniodoma acuminatum*

947 sensu Stein (1883), this is just the procedure that should be used for *Goniodoma* F.Stein,
948 after proposing an illustration of *Goniodoma acuminatum* in Stein (1883) as type.

949 All the members of NCA voted to recommend the proposal (2607) to conserve the
950 name *Heterocapsa* with *H. steinii* Tillmann & al. 2017 as type (Report of the
951 Nomenclature Committee for Algae 22, Andersen 2020). We have to respect the principle
952 of priority and the article 7.3, without the arbitrary inference of the NCA. Stein (1883)
953 proposed the genus *Heterocapsa* F.Stein 1883 for two, and probably three, species that
954 belong to the Kryptoperidiniaceae. Anecdotally, a later isonym, *Heterocapsa* Massart
955 1920, is probably also a member of the Kryptoperidiniaceae. The taxonomical
956 innovations *Heterocapsa steinii* and *Kryptoperidinium triquetrum* are unnecessary. There
957 are no reasons to propose a new type for the genus *Heterocapsa*. The genus *Cachonina*
958 is available for *Heterocapsa triquetra* sensu Stein and congeneric species. This can be
959 solved with the next procedure:

960 *Cachonina monas* (Ehrenberg 1840) *comb. inedit.*

961 Basionym: *Peridinium monas* Ehrenberg 1840, *Ber. K. Akad. Wiss. Berlin* 1840: 201.

962 Heterotypic synonym: *Heterocapsa triquetrum* sensu Stein (1883), *Properidinium*
963 *heterocapsum* Meunier 1919, *Heterocapsa steinii* Tillmann, Gottschling, Hoppenrath,
964 Kusber & Elbrächter 2017.

965 Other congeneric species were already placed in *Cachonina*, and some species will need
966 to be transferred into that genus.

967

968 **6. The case of *Blepharocysta splendor-maris* and *Alexandrium***

969 (2608) Proposal to conserve the name *Peridinium splendor-maris* (*Blepharocysta*
970 *splendor-maris*) (Dinophyceae) with a conserved type. Carbonell-Moore, M.C. (2018).
971 *Taxon* 67: 633–635.

972 (2686) Proposal to conserve the name *Alexandrium* against *Blepharocysta*
973 (Dinophyceae). Elbrächter, M., Gottschling, M., Hoppenrath, M., Jahn, R., Montresor,
974 M., Tillmann, U. & Kusber, W.-H. (2019). *Taxon* 68: 589–590.

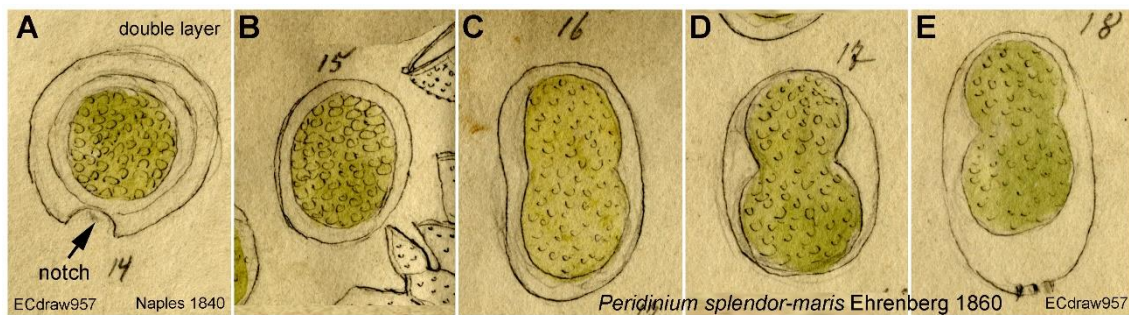
975

976 **6.1. Antecedents**

977 In the nights of August of 1840, Ehrenberg observed a phenomenon of bioluminescence
978 in the shorelines of Naples, Italy. ‘Fortunately’ there were not electric light lamps in 1840.
979 Present day, light pollution does not allow observing the bioluminescence in the

980 overcrowded Mediterranean coasts during the summer. That night, Ehrenberg was unable
981 to observe the plankton sample because the microscope does not work with the light of a
982 candle. An alternative is collecting the sample next morning in the same location, but the
983 assemblage of plankton may change (advection, grazing, vertical migration, etc.), and we
984 will find other organisms that can be mistaken for the truly responsible of the
985 bioluminescence event. Collection of live samples during the night without preservation
986 and the observation hours later imply that the live cells will experience stress-induced
987 morphological changes. Cells of unarmoured dinoflagellates typically lysed, and thecate
988 dinoflagellates may encyst or experience the ecdysis, leaving behind the theca. This is
989 problematic because the typical morphologies of the cells are modified. The aim of
990 Ehrenberg was to identify the organism responsible of the bioluminescence that day of
991 1840. Two decades later, he published the diagnosis of a species named *Peridinium*
992 ‘splendor maris’ (=brilliance of the seas) (Ehrenberg 1860, p. 791). Hereafter, the species
993 epithet will be reported as ‘*splendor-maris*’ using the orthography of the proposal (2608).
994 Thirty-three years after his observations in 1840, Ehrenberg published the illustrations in
995 his illustrations 7–18 as *Peridinium splendor maris* (Ehrenberg 1873) ([ECdraw957,](https://digital.zlb.de/viewer/image/15818596/15/)
996 <https://digital.zlb.de/viewer/image/15818596/15/>). In that publication Ehrenberg cited the
997 name *Blepharocysta* with a short and confusing diagnosis,
998 <https://hdl.handle.net/2027/mdp.39015086629139?urlappend=%3Bseq=20> . A part of
999 the diagnosis can be translated as, “that forms living freely in an envelope belongs to its
1000 own genus for which I propose the name *Blepharocysta*”. A problem is whether we should
1001 consider as valid the description of the genus *Blepharocysta* in Ehrenberg (1873), and
1002 then the type species is reported as *Blepharocysta splendor-maris* (Ehrenberg 1860)
1003 Ehrenberg 1873, or if we should attribute the genus to Stein (1883), reporting the type
1004 species as *Blepharocysta splendor-maris* (Ehrenberg 1860) F.Stein 1883. In the legend
1005 of the plate, Stein (1883) reported, “Fig. 1–16 *Goniodoma acuminatum* Stein (*Peridinium*
1006 *acuminatum* Ehrbg.)” and “Fig. 17–19. *Blepharocysta splendor maris* Ehrbg (z. Theil)”
1007 (zur theil = in part). In the text, Stein (1883, p. 21) reported, “Ehrenberg warf damit noch
1008 andere unklare Formen zusammen”. This evidences that Stein (1883) admitted that
1009 Ehrenberg proposed *Blepharocysta splendor-maris*, and Stein’s illustration tentatively
1010 corresponded to one of the distinct species that Ehrenberg described as *Peridinium*
1011 *splendor-maris*.

1012 Ehrenberg's illustrations 16, 17 and 18 showed individuals under binary division
 1013 inside of a hyaline membrane or capsule (Fig. 10A–E). This mode of division is not the
 1014 usual in gonyaulacoid dinoflagellates (i.e., *Gonyaulax*, *Lingulodinium*, *Alexandrium*,
 1015 *Gessnerium*). The illustration 14 showed a cell inside of a double membrane with an
 1016 apparent concave notch, a feature unknown in dinoflagellates. It is enigmatic to which
 1017 organism corresponds the illustrations 14–18, and it is even doubtful that these line
 1018 drawings correspond to a dinoflagellate (Fig. 10A–E). The etymology of the generic name
 1019 *Blepharocysta* (*blepharos*: eyelid; *kustis*: bladder) refers to this enigmatic organism.

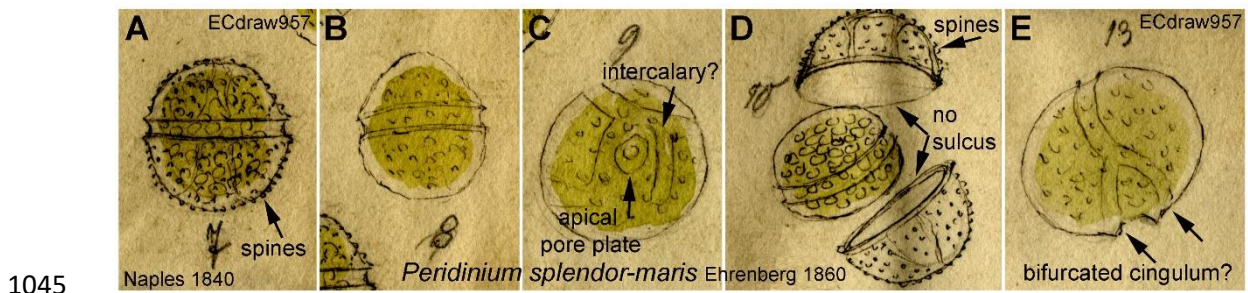


1020

1021 **Fig. 10.** Illustrations of *Peridinium splendormaris*.

1022 Ehrenberg's illustrations 7–10 and 13 show cells devoid of the hyaline membrane
 1023 or capsule (Fig. 11A–E). The illustration 13 showed a globular cell with a kind of
 1024 bifurcated cingulum, a feature unknown in dinoflagellates. The illustrations 7–10
 1025 unequivocally corresponded to dinoflagellates. The illustration 9 showed a cell apparently
 1026 in apical view because there are two central concentric rings that may correspond to the
 1027 apical pore plate (Fig. 11C). As general trend, this kind of circular apical pore plate is
 1028 more commonly found in peridinioid than in gonyaulacoid dinoflagellates. For example,
 1029 the species of *Alexandrium s.l.* have usually a more elongated apical pore. The cell
 1030 showed an elongated plate adjacent to the apical pore plate and parallel to the cingulum
 1031 that is quite atypical in dinoflagellates. It could be interpreted as an atypical elongated
 1032 anterior intercalary plate. The illustration 10 showed a cell that emerged from the empty
 1033 epitheca and hypotheca that split at the cingulum level (Fig. 11D). This evidences that
 1034 Ehrenberg was imprecise in the illustration of the thecal plates. He illustrated the split
 1035 theca as two complete hemispheres. At least one of the hemispheres should be incomplete
 1036 or with a notch at the cingulum level due to the presence of the sulcus. The cingular plates
 1037 were also missing. The cell that emerged from the split theca was antero-posteriorly
 1038 flattened without surface ornamentation (Fig. 11D). The illustration 7 showed a spherical

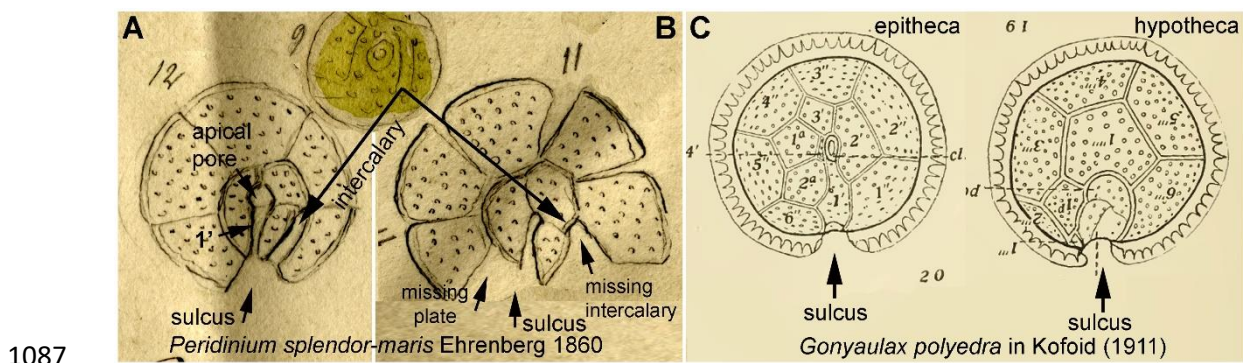
1039 cell with a median cingulum densely covered by short spines (not holes = pores) (Fig.
 1040 11A). The illustration 8 showed a cell with conical epitheca, with a wide and reinforced
 1041 margin of the cingular lists, and missing the thecal ornamentation (Fig. 11B). The
 1042 illustrations 7–10 unequivocally showed dinoflagellate cell, but it is uncertain which
 1043 species because there are numerous peridinioid and gonyaulacoid dinoflagellates with
 1044 similar shape.



1046 **Fig. 11.** Illustrations of *Peridinium splendormaris*.

1047 Ehrenberg's illustration 11 and 12 showed two empty theca with details on the
 1048 shape and ornamentation of the thecal plates (Fig. 12A–B). The first question is whether
 1049 these drawings correspond to the epitheca or hypotheca. Unequivocally, the illustration
 1050 12 corresponds to the epitheca because there is a central circular structure that
 1051 corresponds to the apical pore plate (Fig. 12A). If the illustration 11 belongs to the same
 1052 species, we could consider that it corresponded to the hypotheca because it is distinct
 1053 from that of the illustration 12. The apical pore plate is less evident, the central plates are
 1054 larger, and one of the marginal plates is missing (Fig. 12B). However, the illustration 11
 1055 did not show the typical configuration of the hypothecal plates because the central plates
 1056 are relatively small (a larger central plate is expected). Consequently, it cannot be
 1057 discarded that the illustration 11 may also correspond to the epitheca. Then, the problem
 1058 is that the two epithecae may not belong to the same species. The illustration 12 showed
 1059 five marginal (precingular) plates, but it is more usual is to find six precingular plates.
 1060 The illustration 11 showed six precingular plates if we consider one missing marginal
 1061 plate. The illustration 12 showed an elongated anterior intercalary plate, and the space
 1062 occupied by that plate is also present in the illustration 11. The illustration 12 showed a
 1063 ventral plate lacking ornamentation that corresponded to the typical first apical plate of
 1064 gonyaulacoid dinoflagellates. Then, we can consider that the species has 4 apical, 6
 1065 precingular plates, and an underdetermined number of anterior intercalary plates. This is
 1066 the plate arrangement of the genera *Gonyaulax* or *Lingulodinium*. The species of

1067 *Gessnerium* have three apical plates, and lacked anterior intercalary plates (i.e.,
 1068 *Gessnerium balechii*). This is not the plate arrangement of *Alexandrium* because that
 1069 genus has not anterior intercalary plates (Gómez and Artigas 2019). The illustrations 11
 1070 and 12 showed a cell with scattered large pores and reinforced sutures between the plates
 1071 (Fig. 12A–B). This is a rare feature in the species of *Alexandrium* and *Gessnerium*, while
 1072 more common in *Gonyaulax* and *Lingulodinium*. Jørgensen (1899) already considered
 1073 that some of the Ehrenberg’s illustrations may correspond to *Gonyaulax polyedra* (Fig.
 1074 12C). Charles Kofoid, the most prolific author describing new species of dinoflagellates,
 1075 considered that the illustrations 11 and 12 corresponded to the species *Lingulodinium*
 1076 (= *Gonyaulax*) *polyedra* (Kofoid 1911). Enrique Balech, the most reputed expert on
 1077 tabulation on dinoflagellates, considered that the illustrations 11 and 12 may correspond
 1078 to *Lingulodinium* (= *Gonyaulax*) *polyedra* (Balech 1988). Balech (1988, p. 170) reported,
 1079 “Seguramente Ehrenberg englobó, bajo el nombre *Blepharocysta splendor-maris* (epíteto
 1080 atribuible a la bioluminiscencia de estos organismos) a varios dinoflagelados difíciles de
 1081 referir con seguridad a algunos de los que hoy conocemos. La interpretación personal de
 1082 Stein permitió reconocer a uno como el que hoy conocemos con aquel nombre creado por
 1083 Ehrenberg (que, por tanto, toma como tipo el dibujo de Stein y no los de Ehrenberg).
 1084 Otros de sus dibujos son atribuibles, siempre con dudas, a *Gonyaulax polyedra*. Y es de
 1085 nuevo Stein quien fijó con claridad el aspecto y características más importantes de esta
 1086 especie”.



1088 **Fig. 12.** Illustrations of *Peridinium splendor-maris* and *Gonyaulax polyedra*.

1089 In addition to the morphological aspects, we have to consider the
 1090 bioluminescence. Ehrenberg wanted to identify the organism responsible for the
 1091 brilliance of the sea (*‘splendor maris’*) at Naples that day of 1840. If Ehrenberg was lucky,
 1092 he could observe the real organism responsible of the luminescence. The most common
 1093 dinoflagellate species responsible of bioluminescence are the unarmoured *Noctiluca*

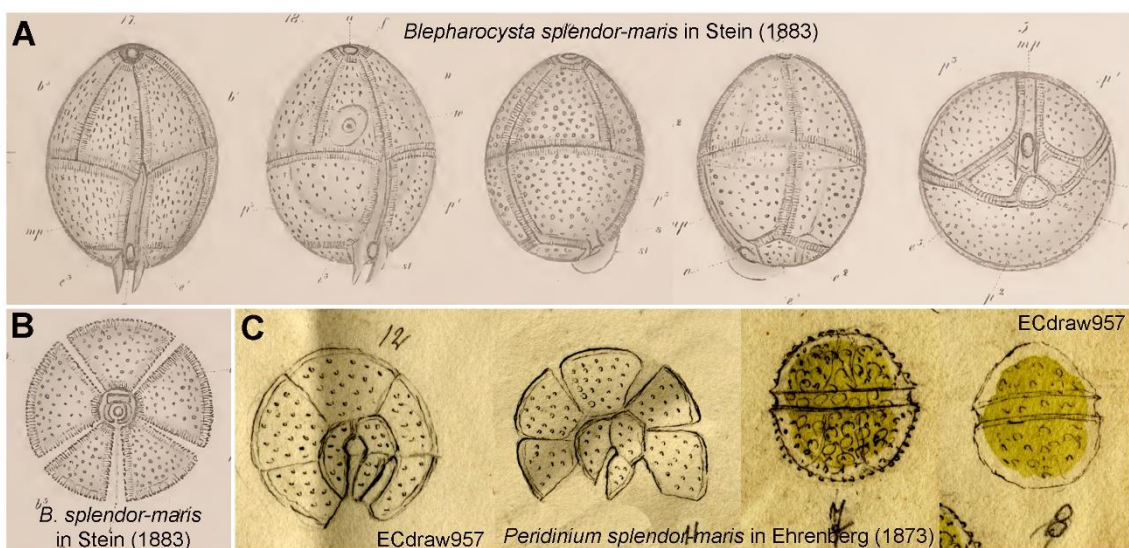
1094 *scintillans*, and the armoured dinoflagellates *Pyrocystis* spp., *Pyrodinium bahamense* and
1095 *Lingulodinium* (= *Gonyaulax*) *polyedra*. *Pyrocystis* is commonly found in the open waters
1096 of tropical seas, and it is not responsible of blooms at the coasts of Naples. *Pyrodinium*
1097 *bahamense* inhabits near the mangles of tropical seas, and that ecosystem and climate are
1098 missing in the Mediterranean Sea. *Lingulodinium polyedra* is a common species in the
1099 Mediterranean Sea (Gómez 2003), and responsible of bioluminescence events in coastal
1100 waters of distinct oceans. The interpretation of Ehrenberg's illustrations is a nightmare
1101 because he provided imprecise line drawings and mixed distinct organisms. It is risky
1102 consider that the illustrations 11 and 12 corresponded to an earlier description of
1103 *Lingulodinium* (*Gonyaulax*) *polyedra*. *Peridinium splendor-maris* is a collective name for
1104 several organisms that appeared associated or after to a bioluminescent event in the
1105 coastal Mediterranean Sea, and Ehrenberg's illustrations did not correspond to species of
1106 *Alexandrium* or *Gessnerium*.

1107

1108 **6.2. Stein's misinterpretation**

1109 Ehrenberg (1873) reported that *Peridinium splendor-maris* was common and abundant in
1110 the Mediterranean Sea. However, it should be taken into account that Ehrenberg
1111 examined few samples, and mainly from eutrophic coastal waters. In contrast, Stein
1112 (1883) observed a distinct dinoflagellate composition after examining samples from the
1113 oligotrophic waters of the open Mediterranean Sea. At Kiel, Baltic Sea, the species
1114 richness is low, and Ehrenberg and Stein may observe the same species. However, in the
1115 Mediterranean Sea where about 1/3 of the known dinoflagellate species have been
1116 recorded (Gómez 2003) is less probable that Ehrenberg and Stein observed the same
1117 species. Stein (1883) read that *Peridinium splendor-maris* was common and abundant in
1118 the Mediterranean Sea, and he tried to accommodate one of his observations to
1119 Ehrenberg's *Peridinium splendor-maris*. Ehrenberg's illustrations 11 and 12 showed an
1120 incomplete theca with three central and five marginal plates (Fig. 12A–B). Stein (1883,
1121 p. 21) reported, “Nach Ehrenberg besteht der Panzer sowohl des Vorder- wie des
1122 Hinterleibes aus fünf seitlichen Tafeln und drei kleineren, nicht über die Peripherie
1123 hervorragenden Endplatten”. Stein looked for a dinoflagellate with three apical and five
1124 precingular plates (Fig. 13B). He found cells belonging to the Podolampadaceae that are
1125 characterized by this atypical plate configuration. Other distinctive characteristic of the
1126 planktonic Podolampadaceae is the lack of the ‘typical’ cingulum composed of

1127 transversally elongated and sunken plates forming the groove that harbours the
 1128 transversal flagellum. Ehrenberg unequivocally illustrated the presence of a cingulum and
 1129 chloroplasts in *Peridinium splendor-maris*, while Stein (1883) illustrated *Blepharocysta*
 1130 *splendor-maris* without cingulum and hyaline cells (he examined fixed samples and the
 1131 pigmentation is lost) (Fig. 13A). Stein's illustrations of *Blepharocysta splendor-maris*
 1132 showed a very distinct shape that *Peridinium splendor-maris*. Even, the relative size and
 1133 shape of the thecal plates, or the presence of sulcal lists in *B. splendor-maris* sensu Stein
 1134 are distinct that in *Peridinium splendor-maris* (Fig. 13C). Unequivocally, Stein's
 1135 illustration of *B. splendor-maris* are unrelated to any of the distinct species that Ehrenberg
 1136 illustrated as *P. splendor-maris*. We can discuss whether the genus name *Blepharocysta*
 1137 was validly published by Ehrenberg (1873) or Stein (1883), but Stein cited *Peridinium*
 1138 *splendor-maris* as basionym of the type of *Blepharocysta* (ICN, art. 7.3). We do not know
 1139 what *Peridinium splendor-maris* sensu Ehrenberg is, but Stein's illustrations are clear and
 1140 precise to facilitate the identification. Further authors have considered *Blepharocysta* for
 1141 the organism illustrated by Stein (1883). A few species of *Blepharocysta* have been
 1142 described because this genus contains low abundant heterotrophic species from the open
 1143 ocean that receives low attention. Carbonell-Moore did observations of *Blepharocysta*
 1144 spp. using scanning electron microscopy, and Gómez et al. (2010) provided the only
 1145 existing molecular data of a species of *Blepharocysta*. There are no major problems. We
 1146 accept that *Blepharocysta* as the species belonging to the genus illustrated by Stein (1883)
 1147 because we do not know what *Peridinium splendor-maris* is.

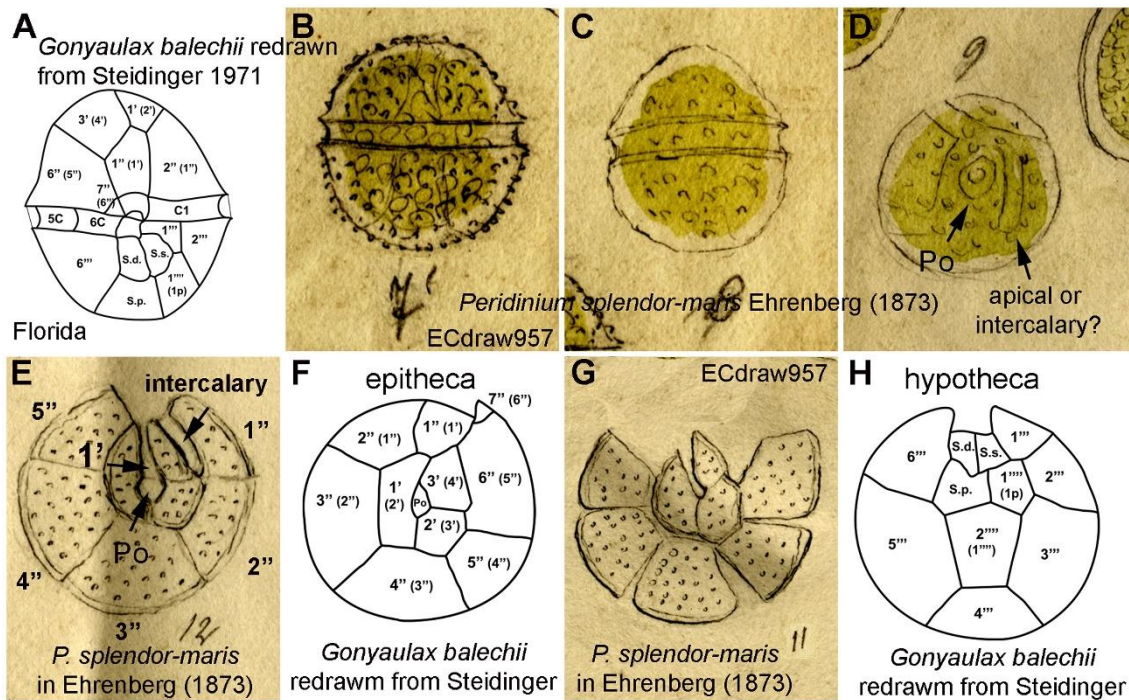


1148

1149 **Fig. 13.** Illustrations of *Blepharocysta* sensu Stein and *Peridinium splendor-maris*.

1150 **6.3. Problem creation**

1151 The *status quo* is broken when Elbrächter et al. in the ‘11th International Conference on
1152 Harmful Algae’ in Cape Town, South Africa, 15–19 Nov 2004, showed a poster entitled
1153 “*Peridinium splendor-maris* Ehrenberg is an *Alexandrium* species but not *Blepharocysta*
1154 *splendor-maris* sensu Stein 1883!”. Elbrächter et al. (2004) considered that the
1155 description of *Blepharocysta splendor-maris* in the summer of 1840 at Naples (Fig. 13B–
1156 E, G) corresponded to the first documented bloom of toxigenic genus *Alexandrium*. If
1157 true, this will be associated with taxonomical innovations because *Blepharocysta* Ehrenberg
1158 1873 has the priority over *Alexandrium* Halim 1960. Elbrächter et al. (2004) also reported
1159 that *Blepharocysta splendor-maris* corresponded to an earlier description of *Gonyaulax*
1160 *balechii*, a taxon later reported as *Pyrodinium balechii* (Steidinger) F.J.R.Taylor 1976,
1161 *Gessnerium balechii* (Steidinger) A.R.Loeblich & L.A.Loeblich 1979 and *Alexandrium*
1162 *balechii* (Steidinger) Balech 1995 (Fig. 14A, F, H). That species was described from
1163 Tampa Bay, Florida, a place with coconut palms and mangrove that is distantly related to
1164 the climate and environmental conditions of the Mediterranean Sea. At Naples, the
1165 researchers of the ‘Stazione Zoologica Anton Dohrn’ have carried out studies on
1166 phytoplankton for over a century with monitoring programs and a culture collection of
1167 microalgae with especial focus on toxic species (*Alexandrium*, *Gessnerium*). However,
1168 there are no documented records of *Gessnerium (Alexandrium) balechii* in the
1169 Mediterranean Sea. There are no strains or molecular data. There are no evidences that
1170 *Gessnerium balechii* was the responsible of a bloom in the summer of 1840 at Naples or
1171 any other bloom in the Mediterranean Sea. None of the Ehrenberg’s illustrations
1172 corresponded to *Gessnerium balechii* or any other species of the genera *Alexandrium* or
1173 *Gessnerium*.



1174

1175 **Fig. 14.** Illustrations of *Peridinium splendormaris* and *Gonyaulax balechii*.

1176 There is no type material of the cells that Ehrenberg observed in 1840. If
 1177 Ehrenberg was able to invent a method to conserve the delicate dinoflagellates, the ICN
 1178 should recommend that method to preserve the type specimens. Obviously, nobody uses
 1179 dried mica to conserve the type specimens of dinoflagellates. Since more than six million
 1180 of years, species of *Alexandrium* or *Gessnerium* have inhabited in the eutrophic coasts of
 1181 the Mediterranean Sea. Any sample from eutrophic coastal waters may potentially contain
 1182 species of *Alexandrium* or *Gessnerium* (i.e., *Gessnerium taylorii*). Ehrenberg's collection
 1183 contains slides of dried mica with samples from distinct locations. Elbrächter et al. (2018)
 1184 examined these slides and selected one the mica #290102-1 as leptoype of *Peridinium*
 1185 *splendormaris* because apparently it contained cells of *Gessnerium*. This is an artificial
 1186 creation of type material. Carbonell-Moore (2018, p. 635) reported, "Ehrenberg (l.c. 1860
 1187 & 1873) did not link any material to a particular slide in either publication, which makes
 1188 it very difficult to be certain that the slides examined by Elbrächter & al. (l.c.) correspond
 1189 in fact to the same material that Ehrenberg described in 1860 and illustrated in 1873".

1190 Elbrächter et al. (2019) submitted the proposal 2686 to conserve *Alexandrium*
 1191 Halim 1960 and to reject *Blepharocysta* Ehrenberg 1873. Elbrächter et al. (2004, 2018)
 1192 considered that *Peridinium splendormaris* is an earlier description of the species first
 1193 described *Gonyaulax balechii* (currently classified in the genus *Gessnerium*, Gómez and

1194 Artigas 2019). Then, the proposal 2686 does not affect to the name *Alexandrium*. More
1195 importantly, there is no evidence to consider that the description of *Peridinium splendor-*
1196 *maris*, the basionym of the generitype of *Blepharocysta*, corresponded to a species of
1197 *Alexandrium* or *Gessnerium*.

1198 The questionable relationship between *Peridinium splendor-maris* and
1199 *Alexandrium/Gessnerium* in Elbrächter et al. (2004, 2018) have motivated the proposal
1200 (2608) to conserve the name *Peridinium splendor-maris* (*Blepharocysta splendor-maris*)
1201 with a conserved type (Carbonell-Moore 2018). Carbonell-Moore concluded, “Finally,
1202 for those accepting Elbrächter & al.’s (l.c.) interpretation of Ehrenberg’s original
1203 material, this proposal avoids the need to replace *Alexandrium* Halim (l.c.) by
1204 *Blepharocysta*”. To assign the type of *Blepharocysta* as one of the illustrations by Stein
1205 (1883) is not necessary because there are no evidences to consider the relationship to
1206 *Alexandrium* or *Gessnerium*. *Peridinium splendor-maris* is a collective name with distinct
1207 species described with imprecise illustrations. However, it is not negative to assign one
1208 of the Stein’s illustrations as type of the genus *Blepharocysta*. Elbrächter et al.’s proposal
1209 is again authored by Dr. Kusber, one of the editors of the ICN, and member of the NCA
1210 that vote the proposals. The NCA may repeat the same error that in the proposal (2382)
1211 on *Peridinium acuminatum* and *Goniodoma*.

1212

1213 **7. The case *Alexandrium catenella* and *A. pacificum***

1214 (2302) Proposal to reject the name *Gonyaulax catenella* (*Alexandrium catenella*)
1215 (Dinophyceae). John, U., Litaker, W., Montresor, M., Murray, S., Brosnahan, M.L.
1216 Anderson D.M. 2014. *Taxon* 63: 932–933.

1217

1218 The consumption of shellfish may result in a syndrome called paralytic shellfish
1219 poisoning that can lead to death. In the 1920s after a toxicity outbreak in California killed
1220 six people and sickened nearly a 100 more (Meyer et al. 1928). The responsible was
1221 identified as the toxins of the dinoflagellate *Gonyaulax catenella* Whedon & Kofoid 1936
1222 (Sommer and Meyer 1937). *Gonyaulax catenella* that lacked anterior intercalary plates
1223 was later classified in the genera *Gessnerium*, *Protogonyaulax* and *Alexandrium*, while
1224 *Gonyaulax* is currently circumscribed to species with anterior intercalary plates.
1225 *Protogonyaulax catenella* (\equiv *Alexandrium catenella*) is the first documented case of a

1226 toxic dinoflagellate. The study of the harmful dinoflagellates blooms is important for
1227 public health, fisheries and aquaculture, and it receives important funds for research.

1228 The molecular data based on the ribosomal RNA gene sequences have
1229 demonstrated that *Protogonyaulax catenella* and its relatives are divided into five groups
1230 (Wang et al. 2014, John et al. 2014a). These ribotypes can be accommodated into five
1231 species names: *Protogonyaulax catenella*, *P. tamarensis*, *P. fundyensis*, *P. mediterranea*
1232 and *P. australiensis*. Although these species were first described from distinct locations,
1233 obviously some of them may overlap in their geographical distributions. For example,
1234 California is the type locality of *Gonyaulax catenella*, but we can also find that species in
1235 the Bay of Fundy, North Atlantic, that is the type locality of *P. fundyensis*, and vice versa
1236 John et al. (2014a) replaced the name *Alexandrium catenella* by the new name
1237 *Alexandrium pacificum* Litaker in John et al. 2014. Contrary to the major principle of
1238 priority, John et al. (2014b) submitted a proposal 2302 to reject *Gonyaulax catenella*.
1239 Fraga et al. (2015), coauthored by Prof. Ø. Moestrup, former a member of the NCA,
1240 published the arguments against the proposal 2302. The proposal was not recommended,
1241 and the Report of the Nomenclature Committee for Algae 15 commented, “*Alexandrium*
1242 *fundyense* and *A. catenella* are certainly conspecific, and then “catenella” has
1243 nomenclatural priority” (Prud’homme van Reine 2017). The NCA should deal on
1244 nomenclature, and the synonymy of the heterotypic synonyms is a subjective topic to be
1245 deal by taxonomists. The molecular data support five species that can be named
1246 *Protogonyaulax catenella*, *P. tamarensis*, *P. fundyensis*, *P. mediterranea* and *P.*
1247 *australiensis*. If the NCA reported that *P. fundyensis* is a synonym of *P. catenella*, then
1248 one of the ribotypes has not any species name.

1249

1250 **8. Final remarks**

1251 The nomenclature deals on the formal naming of the taxa, and it is expected to be
1252 objective as it is regulated by established rules. The ICN has a major principle that is the
1253 priority, and the article 7.3. We should be able to establish the correct names based on
1254 these general rules. However, there is the option to submit proposals to reject or conserve
1255 names (ICN, art. 56.1) when authors consider that a name should prevail against the
1256 general established rules. Then, the 13–15 members of the NCA vote to recommend or
1257 not the proposals. Most of the members of the Nomenclature Committee for Algae work

1258 on macroscopic organisms (macro algae), and they have no experience on dinoflagellate
1259 research. This is not problematic because external evaluators are more objective and
1260 impartial in their decisions than people belonging to the small world of the
1261 dinoflagellates. The problem is that some proposals are based on the taxonomical
1262 interpretations, especially on the scarcely detailed dinoflagellate descriptions of the 19th
1263 century. The publication in a taxonomical journal of a new interpretation of the identity
1264 of one of these earlier dinoflagellates does not mean that the interpretation is fortunate,
1265 and each researcher must evaluate the scientific evidences. This requires experience on
1266 taxonomy of dinoflagellates in order to interpret the line drawings of the original
1267 descriptions, and the style of the earlier microscopists. An example of the taxonomical
1268 contributions on dinoflagellates is the case of Dr. R.A. Andersen, secretary of the NCA
1269 and author of the Report of the Nomenclature Committee for Algae. The genus
1270 *Symbiodinium* Freudenthal 1962 or Gert Hansen & Daugbjerg 2009 is the most
1271 ecologically important dinoflagellate as responsible of the functioning of the coral reefs.
1272 *Symbiodinium* is a thin-walled dinoflagellate typically living as symbiont in marine
1273 benthic invertebrates. This symbiotic microalgae is commonly referred as 'zooxanthella'.
1274 The genus *Zooxanthella* K.Brandt 1881 was proposed for a thecate (peridinioid)
1275 dinoflagellates living in symbiosis with the pelagic planktonic Rhizaria (radiolarians).
1276 There are no morphological or phylogenetical relationships between *Symbiodinium* and
1277 *Zooxanthella*. However, Guiry and Andersen (2018), without own observations, only
1278 added confusion when they transferred all the species of *Symbiodinium* into *Zooxanthella*.

1279 The publication of a taxonomical interpretation in a specialized journal does not
1280 imply that it is correct. The members of the NCA should investigate the taxonomical
1281 bases of each proposal with the due independence, even if they do not care about the
1282 dinoflagellate research. Naming the taxa is regulated by the rules and recommendations
1283 of the ICN, with the priority as major principle, and the article 7.3. If someone disagrees,
1284 there is the option to submit modifications to the ICN. The use of the conservation or
1285 rejection of names should be very exceptional. The NCA is creating arbitrariness and
1286 instability when naming taxa based on questionable taxonomical interpretations.

1287

1288 **9. References**

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