

1 Morphological and phylogenetic data do not support the split of *Alexandrium* into four genera

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3 Kenneth Neil Mertens^{1*}, Masao Adachi², Donald M. Anderson³, Christine Band-Schmidt⁴, Isabel4 Bravo⁵, Michael L. Brosnahan², Christopher J.S. Bolch⁶, António J. Calado⁷, M. Consuelo Carbonell-5 Moore⁸, Nicolas Chomérat¹, Malte Elbrächter⁹, Rosa Isabel Figueroa⁵, Santiago Fraga¹⁰, Ismael6 Gárate-Lizárraga¹¹, Esther Garcés¹², Haifeng Gu¹³, Gustaaf Hallegraeff¹⁴, Philipp Hess¹⁵, Mona7 Hoppenrath¹⁶, Takeo Horiguchi¹⁷, [Mitsunori Iwataki](#)¹⁸, Uwe John¹⁹, Anke Kremp²⁰, Jacob Larsen²¹,8 Chui Pin Leaw²², Zhun Li²³, Po Teen Lim²², Wayne Litaker²⁴, Lincoln MacKenzie²⁵, Estelle Masseret²⁶,9 Kazumi Matsuoka²⁷, Øjvind Moestrup²¹, Marina Montresor²⁸, Satoshi Nagai²⁹, Elisabeth Nézan^{1,30},10 Tomohiro Nishimura²⁵, Yuri B. Okolodkov³¹, Tatiana Yu. Orlova³², Albert Reñé¹², Nagore Sampedro¹²,11 Cecilia Teodora Satta³³, Hyeon Ho Shin³⁴, Raffaele Siano³⁵, Kirsty F. Smith²⁵, Karen Steidinger³⁶,12 Yoshihito Takano³⁷, Urban Tillmann¹⁹, Jennifer Wolny³⁸, Aika Yamaguchi¹⁷, Shauna Murray³⁹

13

14 ¹*Ifremer, LER BO, Station de Biologie Marine, Place de la Croix, BP40537, F-29185 Concarneau*
15 *Cedex, France*16 ²*Laboratory of Aquatic Environmental Science (LAQUES), Faculty of Agriculture and Marine*
17 *Science, Kochi University, 200 Otsu, Monobe, Nankoku, Kochi 783-8502, Japan*18 ³*Woods Hole Oceanographic Institution. Woods Hole, MA 02543, USA*19 ⁴*Departamento de Plancton y Ecología Marina, Instituto Politécnico Nacional, Centro*
20 *Interdisciplinario de Ciencias Marinas (IPN-CICIMAR), La Paz, B.C.S. 23096, Mexico*21 ⁵*Instituto Español de Oceanografía (IEO) and GeoBioTec Research Unit, C.O. Vigo, 36280 Vigo,*
22 *Spain*23 ⁶*Institute for Marine & Antarctic Studies, University of Tasmania, Locked Bag 1370, Launceston TAS*
24 *7250, Australia*25 ⁷*Department of Biology, University of Aveiro, P-3810-193 Aveiro, Portugal*26 ⁸*Department of Botany and Plant Pathology, College of Agricultural Sciences, Oregon State*
27 *University, Corvallis, Oregon 97331-2902, USA*

28 ⁹*Alfred-Wegener-Institut, Helmholtz-Zentrum für Polar- und Meeresforschung Sylt, Hafenstr. 43,*
29 *25992 List/Sylt, Germany*

30 ¹⁰*Praza Mestra Manuela I, 36340 Nigrán, Spain*

31 ¹¹*Instituto Politécnico Nacional, Centro Interdisciplinario de Ciencias Marinas, Apartado Postal 592,*
32 *Col. Centro, La Paz, B.C.S. 23000, Mexico*

33 ¹²*Departament de Biologia Marina i Oceanografia, Institut de Ciències del Mar, Consejo Superior de*
34 *Investigaciones Científicas (CSIC), Pg. Marítim de la Barceloneta 37-49, 08003 Barcelona, Spain*

35 ¹³*Third Institute of Oceanography, Ministry of Natural Resources, Xiamen 361005, China*

36 ¹⁴*Institute of Marine and Antarctic Studies, University of Tasmania, Private Bag 129, Hobart,*
37 *Tasmania 7001, Australia*

38 ¹⁵*Ifremer, DYNECO, Laboratoire Phycotoxines, Rue de l'Île d'Yeu, 44311 Nantes, France*

39 ¹⁶*Senckenberg am Meer, German Center for Marine Biodiversity Research, Wilhelmshaven, Germany*

40 ¹⁷*Department of Biological Sciences, Faculty of Science, Hokkaido University, North 10, West 8,*
41 *Sapporo 060-0810, Hokkaido, Japan*

42 ¹⁸*Asian Natural Environmental Science Center, The University of Tokyo, Bunkyo, Tokyo 113-8657,*
43 *Japan*

44 ¹⁹*Alfred-Wegener-Institut, Helmholtz-Zentrum für Polar- und Meeresforschung, Bremerhaven,*
45 *Germany*

46 ²⁰*Leibniz Institut für Ostseeforschung Warnemünde, Seestr. 15, 18119 Rostock, Germany*

47 ²¹*Marine Biological Section, Department of Biology, University of Copenhagen, Universitetsparken 4,*
48 *DK-2100 Copenhagen Ø, Denmark*

49 ²²*Bachok Marine Research Station, Institute of Ocean and Earth Sciences, University of Malaya,*
50 *16310 Bachok, Kelantan, Malaysia*

51 ²³*Biological Resource Center/Korean Collection for Type Cultures (KCTC), Korea Research Institute*
52 *of Bioscience and Biotechnology, Jeongeup 56212, Republic of Korea*

53 ²⁴*CSS Inc. Under contract to NOS/NOAA, Center for Coastal Fisheries and Habitat Research, 101*
54 *Pivers Island Road, Beaufort, North Carolina 28516, USA*

55 ²⁵*Coastal & Freshwater Group, Cawthron Institute, Private Bag 2, 98 Halifax Street East, Nelson*
56 *7042, New Zealand*

57 ²⁶*MARBEC, Université de Montpellier, CNRS, Ifremer, IRD, Montpellier, France*

58 ²⁷*C/O Institute for East China Sea Research, Nagasaki University, 1551-7 Taira-machi, Nagasaki,*
59 *851-2213, Japan*

60 ²⁸*Stazione Zoologica Anton Dohrn, Villa Comunale, 80121 Naples, Italy*

61 ²⁹*National Research Institute of Fisheries Science, 2-12-4 Fukuura, Kanazawa-ku, Yokohama,*
62 *Kanagawa, 236-8648, Japan*

63 ³⁰*National Museum of Natural History, DGD-REVE, Station de Biologie Marine de Concarneau,*
64 *Place de la Croix, 29900 Concarneau, France*

65 ³¹*Universidad Veracruzana, Instituto de Ciencias Marinas y Pesquerías, Laboratorio de Botánica*
66 *Marina y Planctología, Calle Mar Mediterráneo No. 314, Fracc. Costa Verde, C.P. 94294, Boca del*
67 *Río, Veracruz, México*

68 ³²*A.V. Zhirmunsky National Scientific Center of Marine Biology of the Far Eastern Branch of the*
69 *Russian Academy of Sciences, Palchevskogo Street, 17, Vladivostok 690041, Russia*

70 ³³*Dipartimento di Architettura, Design e Urbanistica, University of Sassari, Via Piandanna 4, 07100*
71 *Sassari, Italy*

72 ³⁴*Library of Marine Samples, Korea Institute of Ocean Science and Technology, Geoje, Republic of*
73 *Korea*

74 ³⁵*Ifremer, DYNECO, PELAGOS, F-29280 Plouzané, France*

75 ³⁶*Florida Fish and Wildlife Conservation Commission Fish and Wildlife Research Institute*
76 *100 8th Avenue SE St. Petersburg, FL 33701, USA*

77 ³⁷*Faculty of Science and Technology, Kochi University, Japan*

78 ³⁸*Maryland Department of Natural Resources, 1919 Lincoln Drive Annapolis, Maryland 21401 USA*

79 ³⁹*Climate Change Cluster, University of Technology Sydney, Ultimo, NSW, 2007, Australia*

80

81 *Corresponding author: Kenneth Neil Mertens

82 E-mail: Kenneth.mertens@ifremer.fr

83 Tel: +33-2-98-10-42-82

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85 **Abstract**

86 A recently published study analyzed the phylogenetic relationship between the genera
87 *Centrodinium* and *Alexandrium*, confirming an earlier publication showing the genus *Alexandrium* as
88 paraphyletic. This most recent manuscript retained the genus *Alexandrium*, introduced a new genus
89 *Episemicolon*, resurrected two genera, *Gessnerium* and *Protogonyaulax*, and stated that: “The
90 polyphyly [*sic*] of *Alexandrium* is solved with the split into four genera”. However, these reintroduced
91 taxa were not based on monophyletic groups. Therefore this work, if accepted, would result in
92 replacing a single paraphyletic taxon with several non-monophyletic ones. The morphological data
93 presented for genus characterization also do not convincingly support taxa delimitations. The
94 combination of weak molecular phylogenetics and the lack of diagnostic traits (i.e., autapomorphies)
95 render the applicability of the concept of limited use. The proposal to split the genus *Alexandrium* on
96 the basis of our current knowledge is rejected herein. The aim here is not to present an alternative
97 analysis and revision, but to maintain *Alexandrium*. A better constructed and more phylogenetically
98 accurate revision can and should wait until more complete evidence becomes available and there is a
99 strong reason to revise the genus *Alexandrium*. The reasons are explained in detail by a review of the
100 available molecular and morphological data for species of the genera *Alexandrium* and *Centrodinium*.
101 In addition, cyst morphology and chemotaxonomy are discussed, and the need for integrative
102 taxonomy is highlighted.

103

104 **Keywords:** taxonomy, phylogenetics, paraphyletic, saxitoxin, spirolides, harmful algal blooms

105

106 **Highlights**

- 107
- Morpho-molecular data do not support the split of *Alexandrium* into four genera.
 - 108 • The genera *Episemicolon*, *Gessnerium*, and *Protogonyaulax* should not be used.
 - 109 • A proposal to conserve *Alexandrium* against *Centrodinium* will be submitted.

110

111 *Introduction and aims*

112

113 The genus *Alexandrium* includes many species that have caused extensive economic and human
114 health impacts worldwide (e.g., Anderson et al., 2012). *Alexandrium* currently encompasses 34
115 accepted species, with *A. camurascutulum* considered invalid (Guiry in Guiry and Guiry, 2020). Of
116 these species, 14 are known to produce paralytic shellfish toxins (PSTs) (Moestrup et al., 2009), which
117 have caused extensive damage to aquaculture industries. The wide range of toxins produced by
118 *Alexandrium* species, belong to four families – PSTs (saxitoxin (STX) and its derivatives), spiroimines
119 (spiroptides and gymnodimines), goniodomins (e.g., Lassus et al., 2016), and lytic compounds (e.g.,
120 Tillmann and John, 2002; Blossom et al., 2019). The toxins with the most recognized potential for
121 economic impact are the PSTs, which are responsible for outbreaks of paralytic shellfish poisoning
122 (PSP), one of the most widespread harmful algal bloom (HAB)-related shellfish poisoning syndromes.
123 PSP outbreaks can cause human illness and death from contaminated shellfish or fish, loss of wild and
124 cultured seafood resources, impairment of tourism and recreational activities, alterations of marine
125 trophic structure, and death of marine mammals, fish, and seabirds (Anderson et al., 2012). Symptoms
126 of PSP in humans range from spreading numbness and tingling sensations, headache and nausea to
127 more extreme fatal cases due to respiratory paralysis (Hallegraeff, 2003). Blooms of species such as
128 *Alexandrium catenella*, *A. minutum*, and *A. pacificum* regularly cause losses of tens of millions of
129 dollars to aquaculture industries in North and South America, Europe, Asia (e.g., Trainer and Yoshido,
130 2014; Sanseverino et al., 2016), and Australia and New Zealand (e.g., Jin et al., 2008; MacKenzie,
131 2014). For example, in late 2012, a single bloom of *A. catenella* along the east coast of Tasmania
132 (Australia) resulted in ~AUD\$ 23 million loss to the wild harvest and aquaculture industries (Condie
133 et al., 2019). Monitoring of *Alexandrium* cells in the water column and of toxins in shellfish is
134 therefore critical for avoidance of adverse effects on human health (e.g., Nagai et al., 2019; EFSA,
135 2009) and nationally and internationally standardized methods have been established to guide PSP
136 testing (e.g., FAO Marine Biotoxins, 2004; [U.S.] National Shellfish Sanitation Program, 2017;
137 Australian Shellfish Quality Assurance Program, 2019; Turner et al., 2019). The European Union

138 requires all its member states to monitor coastal waters for toxin-producing plankton and toxins in
139 mussels (Directive 91/492d/EC and Commission Decision 2002/225/EC). In parallel, research on
140 *Alexandrium* species is vigorous: since 1975, there have been 2,768 published studies that include the
141 word *Alexandrium*, which have been cited 70,322 times, for an average of about 150 publications per
142 year over the last 10 years (Clarivate Analytics search on Web of Science Core Collection on 20
143 August 2020).

144 The taxonomic history of the genus *Alexandrium* is complex, and nomenclatural stability was not
145 attained for some time, as detailed by Balech (1995, pp. 1–3) and Taylor and Fukuyo (1998). The
146 genus *Alexandrium* was erected by Halim (1960) with the PST-producing *Alexandrium minutum* as its
147 type. A few years later, Halim (1967) erected *Gessnerium* with *Gessnerium mochimaense* Halim as its
148 type; this species had a pentagonal first apical (1') plate not in contact with the pore plate (Po).
149 Loeblich III and Loeblich (1979) considered *Alexandrium minutum* to be inadequately described, left
150 it in the genus *Alexandrium* and transferred seven *Gonyaulax* species and two *Goniodoma* species into
151 the genus *Gessnerium*. At the same time, Taylor (1979) erected *Protogonyaulax*, with *P. tamarensis* as
152 the type species and defined it as having a 1' plate directly contacting the Po of the apical pore
153 complex, and transferred eight species of the genus *Gonyaulax* and one *Pyrodinium* species into
154 *Protogonyaulax*. Taylor's proposal was followed by Fukuyo et al. (1985), who described two new
155 *Protogonyaulax* species (*P. affinis* and *P. compressa*). After a detailed examination of samples from
156 the type locality of *A. minutum* (the type species of *Alexandrium*), Balech (1989) noted that plate 1'
157 does not necessarily directly contact the Po in this species (the same applies to *A. fraterculus* and *A.*
158 *kutnerae*). He therefore re-established the genus *Alexandrium*, considering *Protogonyaulax* a junior
159 synonym of *Alexandrium*. All *Protogonyaulax* and *Gessnerium* species were thus transferred to
160 *Alexandrium* (Balech 1985, 1995) and *Gessnerium* was retained as a subgenus of *Alexandrium* for
161 species in which plate 1' is not rhomboidal and does not contact the Po (Balech, 1995). Since Balech
162 (1989), the consensus has been to only use the genus name *Alexandrium*. The currently accepted plate
163 formula for *Alexandrium* is Po, 4', 6'', 6c, 9–10s, 5''', 2'''' (Balech, 1980, 1995; Balech and Tangen,
164 1985).

165 The advent of molecular approaches provided significant contributions to the circumscription
166 of species within this important genus. Morpho-molecular studies suggested that species placed in the
167 subgenus *Gessnerium* do not form a monophyletic group (John et al., 2003; MacKenzie et al., 2004;
168 Kim et al., 2005; Rogers et al., 2006; Penna et al., 2008; Gu et al., 2013). More recently, a detailed
169 study encompassing the morphology of vegetative cells, phylogenies based on multiple molecular
170 markers, mating compatibility and presence/absence of genes coding for STX and analogues has
171 shown that morphological characters used to identify species within the *Alexandrium tamarense*
172 complex (*A. tamarense* and related species) were not consistent, but that molecular markers were able
173 to delineate unambiguous species boundaries (John et al., 2014; but see Fraga et al., 2015 and Litaker
174 et al., 2018).

175 Recently, Li et al. (2019) showed that the fusiform dinoflagellate *Centrodinium punctatum*
176 forms a clade nesting within *Alexandrium*. Through a morpho-molecular study of two other
177 *Centrodinium* species (*C. eminens* and *C. intermedium*), but without a re-investigation of the type, *C.*
178 *elongatum*, Gómez and Artigas (2019) proposed to retain *Centrodinium* and subdivide the species
179 formerly included in the genus *Alexandrium*, sharing a common thecal plate pattern, into four distinct
180 genera, namely *Alexandrium sensu stricto* (s.s.) (emended diagnosis), the re-introduced genera
181 *Gessnerium* and *Protogonyaulax*, and the new genus *Episemicolon*. Here, the data presented in Gómez
182 and Artigas (2019) are critically discussed, and it is shown that they do not support such a drastic
183 taxonomic rearrangement. The aim of this study is not to present an alternative analysis and revision,
184 but to maintain the genus *Alexandrium*. Furthermore, it is emphasized to use integrative taxonomy
185 which delimits taxa using multiple and complementary perspectives (Dayrat, 2005), including the
186 consideration of cyst morphology in recognizing taxa (as previously suggested by Taylor and Fukuyo,
187 1998, p. 6) and chemotaxonomy, amongst other criteria.

188

189 *The presented phylogenetic trees do not support the proposed subdivision of Alexandrium.*

190 The finding that species of *Centrodinium* nest phylogenetically in *Alexandrium* (Li et al.,
191 2019; Gómez and Artigas, 2019) makes the latter paraphyletic. Gómez and Artigas (2019) proposed to
192 taxonomically split *Alexandrium* into four separate genera (not including *Centrodinium*, which never

193 belonged to *Alexandrium*). This proposal establishes a new genus *Episemicolon*, while the diagnosis of
194 three other genera (*Alexandrium*, *Gessnerium*, and *Protogonyaulax*) was emended to group subsets of
195 former *Alexandrium* species. The authors stated that “The polyphyly [*sic*] of *Alexandrium* is solved
196 with the split into four genera”. Notably, *Alexandrium* was not polyphyletic, but paraphyletic. The
197 suggestion that their proposal ‘solved’ this problem is the basis for our critique, and thus it is therefore
198 worth evaluating the phylogenetic information presented by Gómez and Artigas (2019) in detail. Our
199 question was: Does the data justify splitting a phylogenetically well-defined group (e.g., John et al.,
200 2003; Rogers et al., 2006; Orr et al., 2011; Anderson et al., 2012; Baggesen et al., 2012; Gu et al.,
201 2013; Murray et al 2015; Menezes et al., 2018; Kretzschmar et al., 2019), sharing the same Kofoidian
202 plate tabulation, into segregate genera?

203 Gómez and Artigas (2019) presented two phylogenetic trees, Fig. 4 a phylogenetic analysis of
204 alignments of the SSU (18S) region of the rRNA operon and Fig. 5 the D1–D2 region of the LSU
205 (28S) region of the rRNA operon. Each alignment was analyzed using a maximum likelihood (ML)
206 approach and clades were given with bootstrap support. There was no information on the number of
207 base pairs analyzed, the number of informative sites, and the alignments were not made available for
208 evaluation. These phylogenetic analyses are problematic for several reasons:

209

210 1. In their Fig. 5, the phylogeny using the D1–D2 regions of rRNA, which are generally ~600 bp in
211 length, the proposed *Alexandrium s.s.* and *Protogonyaulax* are polyphyletic. In their Fig. 4, the
212 phylogeny using (presumably) partial SSU regions of rRNA, of an unknown length, *Protogonyaulax*,
213 *Episemicolon* and *Alexandrium s.s.* are all para- or polyphyletic. In other words, based on their own
214 analysis, the authors propose the replacement of a single paraphyletic taxon (*Alexandrium*) with
215 several non-monophyletic ones. The generic concepts are not substantiated by the molecular data.
216 Thus, rather than solving the taxonomic problems, they exacerbate them.

217

218 2. There is very little genetic difference between species of *Centrodinium* and *Episemicolon*. In a
219 comparison of sequences of *C. punctatum* in the NCBI database, a difference of < 1% and < 5% was
220 found between it and *A. affine* in aligned sequences of SSU and LSU rRNA, which was less than the

221 genetic differences among species of *Centrodinium*. Species that are highly similar in molecular
222 genetic sequences of rRNA genes, with identical tabulation when considering plate homologies, need
223 exceptionally different other autapomorphies in order to be placed in separate genera, and little
224 evidence of this is found (see below).

225

226 3. The Gómez and Artigas (2019) phylogenies have used short alignments with too few characters and
227 taxon information to accurately infer deeper, clade level branchings within the genus *Alexandrium*
228 which will be stable into the future. Of the major factors that impact the accuracy of phylogenetic
229 inference, two are particularly important: the length of aligned sequence/number of genes used, and
230 the taxon sampling. Past studies of *Alexandrium* phylogenetics were reviewed (Table 1, John et al.,
231 2003; Leaw et al., 2005; Rogers et al., 2006; Orr et al., 2011; Anderson et al., 2012; Baggesen et al.,
232 2012; Gu et al 2013; Murray et al., 2014; Murray et al., 2015; Menezes et al., 2018; Gottschling et al.,
233 2020), and this showed that clades within *Alexandrium* differed depending on gene and taxon
234 sampling (exemplified by basal clades shown in Table 1). All else being equal, more sequence data
235 and greater taxon sampling generally leads to more accurate and well-supported phylogenies. Murray
236 et al. (2015) conducted an analysis of *Alexandrium* using a concatenated alignment of eight genes,
237 with a total length of 7308 bp. The position of several of the major clades of *Alexandrium* differed in
238 that analysis, compared to the analysis presented by Gómez and Artigas (2019). Similarly, new
239 ribotypes are still being reported, such as *Alexandrium fragae* (Branco et al., 2020) and three new
240 phylotypes nested within the genus (Nishimura et al., in review). It is likely that these new discoveries
241 and longer alignments/greater gene sampling will lead to more strongly supported phylogenies than
242 those of Gómez and Artigas (2019), whose phylogenies appear to be too weak to support taxonomic
243 rearrangements.

244 As any taxonomic rearrangement of *Alexandrium* will potentially impact hundreds or
245 thousands of scientists, government regulators, and the seafood industry, it is crucial that the
246 phylogenetic basis for such a change be exceptionally clear, highly stable, and reproducible by other
247 scientists. However, this has not occurred in this case. Gómez and Artigas (2019) have not provided
248 access to their alignment or details of their analytical output. Dinoflagellate lineages display major

249 differences in evolutionary rates in ribosomal RNA genes, particularly in the gonyaulacoid lineage.
250 Examples of this can be seen in Orr et al. (2012), Gu et al. (2013) and Gottschling et al. (2020), in
251 which the species of the Gonyaulacales are generally present on much longer branches than most other
252 clades of dinoflagellates, a difference not seen in analyses using nuclear genes (e.g., Kretzschmar et
253 al., 2019). While Gómez and Artigas (2019) selected a potentially suitable model for their ML
254 analyses, inclusion of divergent taxa can still lead to misplacement of taxa/clusters, with high support
255 values, due to various long-branch effects (Kück et al., 2012). No phylogeny-testing (such as leave-
256 one-out testing and jackknifing by species/clusters) apart from the bootstrap support was used to
257 determine whether the branch order of taxa/clusters was stable or unaffected by long-branch artifacts.

258

259 *The morphological concepts of the reinstated and emended genera proposed by Gómez and Artigas*
260 *(2019) have little taxonomic value*

261 As mentioned in the introduction, *Protogonyaulax* was described by Taylor (1979) as having a
262 plate 1' in contact with the Po. As remarked by Balech (1989, p. 210) for the type species of
263 *Alexandrium*, *A. minutum*, as well as for *A. fraterculus* and *A. kutnerae*, this feature is variable, and the
264 plate 1' can have an indirect contact with the Po through a filiform prolongation of plate 1'
265 (*Alexandrium acatenella*, *A. andersonii*, *A. ostenfeldii*, *A. tropicale* are additional examples; Balech,
266 1995). Gómez and Artigas (2019) considered species exhibiting only a direct contact of plate 1' to the
267 Po as belonging to their emended concept of *Protogonyaulax*, and species with direct or indirect
268 contact (presumably meaning displaying both types) as belonging to their emended genus
269 *Alexandrium*. However, when reviewing the literature, it is clear that there is no consistency with the
270 application of both genus concepts (Table 2); furthermore, the high variability of the contact between
271 plate 1' and Po within *Alexandrium* species speaks against considering this as a reliable taxonomic
272 character. In addition, Gómez and Artigas (2019) describe the 6'' plate as being “usually narrow” in
273 *Alexandrium s.s.*, however, this is not so in *A. insuetum*, *A. ostenfeldii*, and *A. tamutum*, species which
274 are retained in *Alexandrium s.s.* in their proposed phylogeny. Finally, the posterior sulcal plate (Sp) of
275 the emended genus *Protogonyaulax* is longer than wide, and in *Alexandrium s.s.* wider than long, but
276 the Sp of *A. leei*, included in *Protogonyaulax*, is wider than long and in *A. margalefii*, included in

277 *Alexandrium s.s.*, longer than wide with an extremely oblique anterior margin (Balech, 1995). In
278 summary, the considerations of Balech (1995) which support synonymization of *Protogonyaulax* with
279 *Alexandrium*, still stand.

280 The reinstated genus *Gessnerium* also presents problems. Gómez and Artigas (2019) included
281 within this genus species with a pentagonal plate 1' not in contact with the Po. They excluded three
282 species with a plate 1' not in contact with the Po from their concept of *Gessnerium*: *A. insuetum*, which
283 they included in *Alexandrium s.s.* despite the fact that this species has a pentagonal 1' plate that does
284 not touch the Po (Balech, 1995, Plate XVII, Figs. 1–23), and *A. pohangense* and *A. margalefii*, which
285 were not formally attributed to any genus, although were assigned to the *Alexandrium s.s.* clade in
286 their Fig. 4. The authors considered the quadrangular plate 1' of *A. pohangense* and *A. margalefii* as a
287 unique character distinguishing them from the other *Gessnerium*. However, the plate 1' in *A.*
288 *pohangense* has a short suture with plate 2' and can therefore be considered pentagonal (Lim et al.,
289 2015, their Fig. 4B), and such a short suture can also be observed in *A. balechii* and *A. foedum*
290 according to Balech (1995, p. 103), which were classified as *Gessnerium* by Gómez and Artigas
291 (2019). Within *A. taylorii*, the plate 1' is known to vary between a quadrangular and pentagonal shape
292 (Delgado et al., 1997). The infraspecific variability of the shape of this plate indicates that it cannot be
293 used as a diagnostic character at the genus level (Table 2). Finally, the Sp of the emended genus
294 *Gessnerium* is longer than wide and extending obliquely, but in *A. monilatum*, which is included in
295 this genus, the Sp is rhomboid (Balech, 1995).

296 The main diagnostic character of the new genus *Episemicolon* is the presence of an anterior
297 attachment pore placed on the dorsal side of the apical pore plate. However, in *A. gaarderae* the
298 anterior attachment pore is defined as semi-dorsal (Larsen and Nguyen-Ngoc, 2004) and in *A.*
299 *monilatum*, included in *Gessnerium*, the anterior attachment pore is slightly to the right of the dorsal
300 side (Balech, 1995). Moreover, *A. concavum*, which also has a semi-dorsal attachment pore (Larsen
301 and Nguyen-Ngoc, 2004) was placed in *Gessnerium* by Gómez and Artigas (2019). There is presently
302 insufficient evidence to accept the location of the anterior attachment pore in the apical pore plate as a
303 diagnostic character to separate these taxa at the generic level from other *Alexandrium* species. In
304 addition, Gómez and Artigas (2019) claim that the shape of the apical pore of *Episemicolon* is unique

305 because it is “oval or bullet” (their Table 1, as “Shape of apical pore plate”) which is incorrect because
306 it is comma-shaped (Larsen and Nguyen-Ngoc, 2004), just like other *Alexandrium* species.

307 The tabulation of the genus *Centrodinium*, as displayed in *Centrodinium punctatum*, is
308 identical to that of *Alexandrium* when taking into account plate homologies (Li et al., 2019). It can not
309 be excluded that some of the differences listed by Gómez and Artigas (2019) such as the shape of the
310 apical pore, the presence of a pore in the anterior sulcal plate, etc., could be sufficient to separate this
311 taxon on a subgeneric level. More detailed morphological information on the type species of
312 *Centrodinium*, *C. elongatum*, is however required. The large variation in tabulation reported in species
313 of *Centrodinium* by Hernández-Becerril et al. (2010, see their Table 1 for a summary) indicates that
314 further investigation into this genus is needed to properly report on its phylogenetic placement.

315 In summary, the morphological concepts used to separate the reinstated genera from
316 *Alexandrium s.s.* are highly variable and insufficient to justify a split of the genus *Alexandrium*. There
317 is also insufficient morphological evidence to decide whether *Episemicolon* and *Centrodinium* warrant
318 separate generic names.

319

320 *The cyst morphology does not support the new genera*

321 Cysts of *Alexandrium* are morphologically diverse (Table 2) and different from cysts of
322 closely related genera, such as *Pyrodinium*, which has process-bearing cysts (e.g., Wall and Dale,
323 1968, pp. 102–103) or *Fragilidium*, which has a very thick layer of mucus (12–18 µm; Owen and
324 Norris, 1985). Cyst morphology can serve to subdivide genera, as has been proposed for the genus
325 *Protoperidinium* (Harland, 1982). Because cysts are well-known within the genus *Alexandrium* (e.g.,
326 Bolch et al., 1991; Matsuoka and Fukuyo, 2000; Bravo et al., 2006), they should be taken into account
327 for the best possible integrative taxonomy. Since there is no consistent cyst morphology that can be
328 associated with any of the genera proposed by Gómez and Artigas (2019), cyst morphology also does
329 not unambiguously support the subdivision of *Alexandrium* into these genera.

330

331 *There is no evident relationship of the proposed genera to toxin production (chemotaxonomy).*

332 Toxin production has long been considered to be a character independent of chemical taxonomy
333 because the same toxins have been described in very distantly related dinoflagellate genera, e.g.,
334 okadaic acid in *Prorocentrum* spp. and *Dinophysis* spp., STX or analogs in *Alexandrium* spp.,
335 *Gymnodinium catenatum*, *Pyrodinium bahamense* as well as in several cyanobacterial species (e.g.,
336 *Aphanizomenon flosaquae* and *Lyngbya wollei*), or domoic acid which is produced in several diatom
337 genera of *Pseudo-nitzschia* and *Nitzschia*, as well as in the macroalga *Chondria armata*.

338 For the genera in question here, three toxin groups are worth considering for chemotaxonomy:
339 saxitoxins (STXs), spiroimines (spiroolides and gymnodimines) and goniodomins. Based on John et al.
340 (2014), Murray et al. (2015), Lassus et al. (2016), Lugliè et al. (2017), and Branco et al. (2020), STX
341 or analogs are produced by 14 *Alexandrium* species (*A. acatenella*, *A. affine*, *A. andersonii*, *A.*
342 *australiense*, *A. catenella*, *A. cohorticula*, *A. fragae*, *A. leei*, *A. minutum*, *A. ostensfeldii*, *A. pacificum*,
343 *A. tamarense*¹, *A. tamiyavanichii*, *A. taylorii*), which do not form a clear monophyletic cluster (Murray
344 et al., 2015, Fig. 1). Due to the spread of STX-production across a range of phylogenetically different
345 *Alexandrium* species, STX-production in this genus appears to be very common but it is not clear
346 whether it should be considered a coherent taxonomic feature for this genus. The increasing number of
347 STX analogues should be systematically re-verified in a large number of geographically diverse
348 strains, with the limits of detection (LOD) and quantification (LOQ) provided.

349 Spiroimines are solely known to be produced by *Alexandrium ostensfeldii* (= *Alexandrium*
350 *peruvianum*; Kremp et al., 2014; Zurhelle et al., 2018).

351 Goniodomins have been reported to be produced by *Alexandrium monilatum*, *Alexandrium*
352 *hiranoi* and *Alexandrium pseudogonyaulax* (Harris et al., 2020).

353 Overall, it should be noted that many papers only report positive presence of toxins in a strain
354 but not the LOD or LOQ for those analogues that were not discovered. There are few studies
355 systematically reporting comparative presence of analogues in a wide range of species, e.g. Wiese et
356 al. (2010), for STX group toxins. However, spiroolides have not been systematically searched in most

1 Following the taxonomic concept of *A. tamarense* of John et al. (2014), only one strain of *A. tamarense* is
2 currently considered to produce low amounts of gonyautoxins (Lugliè et al., 2017).

357 *Alexandrium* species and goniodomins have been largely overlooked other than in the three species
358 mentioned above.

359

360 *Conclusions*

361 The data presented by Gómez and Artigas (2019) are insufficiently robust to form the basis on
362 which to subdivide species of the genus *Alexandrium* into four different genera, and maintain
363 *Centrodinium*. Resolving consistent generic-level clusters within the genus *Alexandrium* and across
364 the gonyaulacoids more generally, would require additional detailed morphological re-investigations
365 and more extensive multigene phylogenies, with careful attention to rigorous testing of taxon sampling
366 effects, branching order stability, long-branch effects, and careful selection of appropriate multiple
367 outgroups for rooting local versus global dinoflagellate phylogenies. A secondary structure analysis of
368 a more expanded dataset could also be beneficial. Inclusion of cyst morphology and chemotaxonomic
369 information should also be strived for. There is an extensive literature on *Alexandrium* species and this
370 is a very active area of research. If the proposal of Gómez and Artigas (2019) is adopted there will be
371 considerable disruption and confusion to this field of study.

372 Therefore, here it is recommended to continue using the generic name *Alexandrium* for
373 species of this complex, and to refrain from using *Protogonyaulax*, *Gessnerium*, and *Episemicolon*.
374 The proposals by Gómez and Artigas (2019), if adopted, would introduce taxonomical instability into
375 this group of species. A proposal to conserve *Alexandrium* against *Centrodinium* will be submitted to
376 the International Nomenclature Committee for Algae (INA) in parallel to this note. The nomenclatural
377 stability has particular importance as many species of *Alexandrium* cause harmful algal blooms and
378 produce potent biotoxins. In addition to the biological scientific community the generic name
379 *Alexandrium* is used also by chemists, medical scientists such as toxicologists, veterinarians, seafood
380 safety regulators, fisheries and aquaculture industry personnel, administrators, and environmental and
381 fisheries policy makers as outlined by Litaker et al. (2018). Furthermore, *Alexandrium* species are an
382 important component of planktonic assemblages and taxonomic changes can create confusion for
383 climate change studies and interpretations of long-term data sets. Finally, it is recommended that
384 morphological criteria used to separate taxa are unambiguous and leave no room for doubt in the

385 attribution of taxa (cf. paragraph 1 of the preamble of the ICN, Turland et al., 2018), that authors make
386 their alignments freely available to allow for coherent progress in the field, and that authors strive for
387 integrative taxonomy (Dayrat, 2005). Conservation of taxon names has been promoted across all
388 organisms, to avoid taxonomic anarchy (Garnett and Christidis, 2017). As such, taxonomists should
389 aim to conserve original names as much as possible and new taxa and combinations should only be
390 created when robust morpho-molecular data obliges it (cf. paragraph 12 of the preamble of the ICN,
391 Turland et al., 2018).

392

393 **Acknowledgements**

394 Support to DMA from the NOAA ECOHAB program (Grant #NA15NOS4780181) is gratefully
395 acknowledged. Support to EG, AR, NS from the COPAs project (CTM2017-86121-R) is
396 acknowledged. Marc Gottschling is acknowledged for interesting and civil discussions. Two
397 anonymous reviewers are acknowledged for their useful comments.

398

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