

1
2 DR. FREDERIK LELIAERT (Orcid ID : 0000-0002-4627-7318)

3
4
5 Article type : Research Article

6
7
8 ***Brilliantia kiribatiensis*, a new genus and species of Cladophorales**
9 **(Chlorophyta) from the remote coral reefs of the Southern Line Islands, Pacific**
10 **Ocean¹**

11 Frederik Leliaert²

12 Meise Botanic Garden, 1860 Meise, Belgium

13 Emily L. A. Kelly²

14 Center for Marine Biodiversity and Conservation, Scripps Institution of Oceanography, University
15 of California San Diego, La Jolla, California 92037, USA

16 Jan Janouškovec

17 Department of Biology, San Diego State University, San Diego, California 92182, USA

18 Centre Algatech, Institute of Microbiology of the Czech Academy of Sciences, Novohradská 237,
19 37901 Třeboň, Czech Republic

20 Michael D. Fox, Maggie D. Johnson

21 Center for Marine Biodiversity and Conservation, Scripps Institution of Oceanography, University
22 of California San Diego, La Jolla, California 92037, USA

23 Woods Hole Oceanographic Institution, 266 Woods Hole Rd, Woods Hole, Massachusetts 02543,
24 USA

25 Farran M. Redfern

This article has been accepted for publication and undergone full peer review but has not been through the copyediting, typesetting, pagination and proofreading process, which may lead to differences between this version and the [Version of Record](#). Please cite this article as [doi: 10.1111/JPY.13230](#)

This article is protected by copyright. All rights reserved

26 Environment and Conservation Division, Ministry of Environment Lands and Agriculture
27 Developments, P.O. Box 234 Bikenibeu, Tarawa, Kiribati

28 Taati Eria

29 Ministry of Fisheries and Marine Resources Development, PO Box 64 Bairiki, Tarawa, Kiribati

30 Andreas F. Haas

31 NIOZ Royal Netherlands Institute for Sea Research and Utrecht University, Den Burg, Texel 1790
32 AB, The Netherlands

33 Enric Sala

34 Pristine Seas, National Geographic Society, Washington, DC 20036, USA

35 Stuart A. Sandin, Jennifer E. Smith²

36 Center for Marine Biodiversity and Conservation, Scripps Institution of Oceanography, University
37 of California San Diego, La Jolla, California 92037, USA

38
39 ¹Received __. Accepted __.

40 ²Authors for correspondence: e-mail frederik.leviaert@meisebotanicgarden.be,
41 emilylak@gmail.com, smithj@ucsd.edu

42 *Frederik Leliaert and Emily L. A. Kelly are co-first authors of the paper.

43 **Running title:** *Brilliantia kiribatiensis* gen. et sp. nov.

44
45 Editorial Responsibility: O. De Clerck (Associate Editor)

46 **ABSTRACT**

47 The marine green alga *Brilliantia kiribatiensis* gen. et sp. nov. is described from samples collected
48 during two expeditions (2009, 2013) from the coral reefs of the Southern Line Islands, Republic of
49 Kiribati, Pacific Ocean. Phylogenetic analysis of sequences of the large- and small-subunit rDNA
50 and the rDNA internal transcribed spacer region revealed that *Brilliantia* is a member of the
51 Boodleaceae (Cladophorales), containing the genera *Apjohnia*, *Boodlea*, *Cladophoropsis*,
52 *Chamaedoris*, *Phyllocladion* and *Struvea*. Within this clade it formed a distinct lineage, sister to
53 *Struvea elegans*, but more distantly related to the bona-fide *Struvea* species (including the type *S.*
54 *plumosa*). *Brilliantia* differs from the other genera by having a very simple architecture forming
55 upright, unbranched, single-celled filaments attached to the substratum by a rhizoidal mat. Cell
56 division occurs by segregative cell division only at the onset of reproduction. Based on current
57 sample collection, *B. kiribatiensis* seems to be largely restricted to the Southern Line Islands,
58 although it was also observed on neighboring islands, including Orona Atoll in the Phoenix
59 Islands of Kiribati, and the Rangiroa and Takapoto Atolls in the Tuamotus of French Polynesia.
60 This discovery highlights the likeliness that there is still much biodiversity yet to be discovered
61 from these remote and pristine reefs of the central Pacific.

62 **Key words:** 18S nuclear ribosomal DNA; Chlorophyta; Cladophorales; molecular phylogeny;
63 Siphonocladales; Ulvophyceae

64 **Abbreviations:** BISH, Bishop Museum; ML, maximum likelihood; SCR, Herbarium of Scripps
65 Institution of Oceanography, University of California; SLIMPA, Southern Line Island Marine
66 Protected Area.

67 INTRODUCTION

68 The Southern Line Islands in the central Pacific Ocean are some of the most remote islands on
69 earth. They form the southern half of the Line Islands Archipelago in the Republic of Kiribati and
70 consist of five islands and atolls: Flint, Vostok, Starbuck, Malden, and Millennium Atoll (known
71 as Caroline Atoll prior to 2000). They are currently uninhabited and are seldom visited, with a
72 history of sporadic human settlement. Having significant biodiversity value, the atolls and their
73 coral reefs are considered some of the most pristine on the planet (Sandin and Charles 2009,
74 Barott et al. 2010, Smith et al. 2016, Mangubhai et al. 2019). Information on marine biodiversity
75 in these atolls, however, is fragmented (Kerr and Wragg 2008), and data on benthic macroalgal
76 diversity is almost non-existent.

77 Limited surveys from the neighboring Northern Line Islands, including Palmyra Atoll,
78 Jarvis Island, and Kingman Reef indicate a relatively low diversity of seaweeds, including six
79 brown algae (Phaeophyceae), 28 green algae (Chlorophyta), and 83 red algae (Rhodophyta;
80 Sandin et al. 2008, Braun et al. 2009, Tsuda et al. 2012). Many of these species were found to be
81 widely recorded in the tropical Indo-Pacific, while a few others had narrower ranges within
82 Polynesia.

83 Among the green algae reported from the Line Islands, species of Cladophorales are well
84 represented with eleven species of *Cladophora*, *Cladophoropsis*, *Dictyosphaeria*, *Microdictyon*,
85 *Phyllodictyon* and *Valonia* (Tsuda et al. 2012). Similar to the other algal groups, most of the
86 members of the Cladophorales have broad tropical ranges, with the exception of *Microdictyon*
87 *setchellianum*, which is restricted to the Pacific Islands of Polynesia, Micronesia, French
88 Polynesia, and Hawaii (Guiry and Guiry 2021). Tropical species of Cladophorales often have wide
89 ranges as a result of high dispersal capacity (Leliaert et al. 2009b). Still, there are numerous
90 species with more confined ranges. For example, *Struvea gardineri* and *Phyllodictyon orientale*
91 are restricted to some Indian Ocean islands, *Struvea thoracica* occurs only in the Great Barrier
92 Reef and New Caledonia, and *Struvea okamurae* is restricted to the Philippines, Japan, and a few
93 other Pacific islands (Leliaert and Coppejans 2007).

94 The Cladophorales is a diverse order of about 500 species in 32 genera, which have been
95 traditionally distinguished by their thallus architecture and more recently through molecular

96 phylogenetic analyses (Leliaert et al. 2007a, Boedeker et al. 2016). The order is predominantly
97 marine with a number of species occurring in freshwater habitats (Škaloud et al. 2018). Most
98 species are macroscopic, although recently a number of microscopic species have been assigned to
99 the order based on DNA sequence data (Leliaert et al. 2009a, Johnston et al. 2018). Species in the
100 Cladophorales are characterized by a siphonocladous thallus architecture, which means that the
101 multicellular thalli are composed of multinucleate cells with regularly-spaced nuclei in a stationary
102 cytoplasm, and multiple chloroplasts are interconnected by delicate strands forming a parietal
103 network or a more or less continuous layer (McNaughton and Goff 1990). The basic thallus
104 architectures are branched or unbranched filaments, but tropical marine species exhibit a
105 remarkable diversity of morphologies, including blade- and net-like forms, as well as giant-celled
106 thalli with unique cytomorphological traits and modes of cell division (Mine et al. 2008). The
107 Boodleaceae (sensu Huisman and Leliaert 2015; *Chamaedoris* clade sensu Leliaert et al. 2007) is
108 one of the most diverse clades morphologically, including cushion-like forms (*Boodlea*,
109 *Cladophoropsis*), net-like blades with stipes (*Struvea*, *Phyllodictyon*), and stipitate capitula
110 (*Apjohnia*, *Chamaedoris*).

111 Expeditions in 2009 and 2013 to the remote Southern Line Islands (Fig. 1, a and b) were
112 undertaken with the primary goal of categorizing reef community structure and productivity
113 (Smith et al. 2016, Fox et al. 2018, Johnson et al. 2020). During these surveys we observed a
114 conspicuous and common green alga composed of densely clustered, stiff, erect unbranched
115 single-celled filaments attached to coral or rocky substrate with a matted rhizoidal mass. The erect
116 filaments could have crustose coralline algae and other epiphytes toward the base. The algae had a
117 siphonocladous appearance but could not readily be assigned to any of the known species or
118 genera of Cladophorales. Here we describe the morphology, ecology, geographical distribution,
119 and phylogenetic relationships of this undescribed species, which also represents a new genus.

120

121 **MATERIALS AND METHODS**

122 *Sampling, morphological observations, and species distribution*

123 Sample collections and surveys were done under two Scientific Research Permits issued by the
124 Republic of Kiribati for March 24 – May 5, 2009 and October 9 – November 15, 2013. All

125 collections were obtained using SCUBA, and samples were photographed fresh on board the
126 research vessel, pressed as herbarium specimens, and preserved in 4% formalin/seawater. Clean
127 portions of the thalli were desiccated and stored in silica gel for subsequent molecular analysis.
128 Voucher specimens, including holo- and paratypes, are deposited at the Bernice Pauahi Bishop
129 Museum's Herbarium Pacificum (BISH), and additional specimens are housed in the herbarium of
130 the Scripps Institution of Oceanography, University of California (SCR). Specimens were
131 examined with an Olympus 40 bright field light microscope and an Olympus 16ZXstereo
132 microscope, and photographs were taken with an integrated Olympus 10 MP digital camera
133 mounted on the light or stereo microscope. Three measurements of the thallus were taken on
134 preserved and dried specimens collected from each island: range in diameter of the stipe, range in
135 diameter of the rhizoids, and total height of the alga.

136 Distribution and abundance of the new species and the composition of the algal community
137 of Flint, Vostok, Starbuck, Malden, and Millennium (Fig. 1) were determined through a series of
138 photographic benthic surveys conducted around each island. Varying based on island
139 circumference, 6-14 survey sites were established at each island. Photoquadrats (1 m²) were taken
140 every 2 m along a 25 m belt transect at 10 m depth at each site. Photographs were analyzed using
141 the image analysis program PhotoGrid 1.0 in which 100 stratified random points per photo were
142 identified to genus level for fleshy macroalgae or functional group for turf algae, crustose coralline
143 algae, and cyanobacteria. The percent cover of the new cladophoralean species and other algal
144 groups were recorded for each site at all five islands (Table S1 in the Supporting Information).

145 Additional observations were made and photographs were taken from Orona Atoll,
146 Phoenix Islands (Kiribati) in May 2018, and from the Rangiroa and Takapoto Atolls, Tuamotus
147 (French Polynesia) in September 2021.

148

149 *DNA sequencing and phylogenetic analyses*

150 In order to determine the phylogenetic affiliation of the cladophoralean species from the Southern
151 Line Islands, we inferred molecular phylogenetic analyses based on partial small subunit (SSU)
152 and large subunit (LSU) rDNA, and rDNA internal transcribed spacer (ITS1-5.8S-ITS2)
153 sequences derived from a sample collected off the coast of Millennium Island, on 11 September

154 2013. Total genomic DNA was extracted by using Power Soil DNA Extraction Kit following the
155 manufacturer instructions, with a 10 min vortexing step. SSU rDNA was amplified (annealing for
156 30 s at 52°C and extension for 2 min at 72°C for 35 cycles) by the universal eukaryotic primers
157 Euk-A 5'-AACCTGGTTGATCCTGCCAGT-3' (Medlin et al. 1988) and 18SRU 5'-
158 CWGGTTCACCWACGGAAACCTTGTTACG-3' (Tikhonenkov et al. 2016), gel-purified, and
159 cloned by using the pGEM-T PCR cloning vector (Promega) in One Shot TOP10 E. coli
160 (Invitrogen). Ten bacterial clones were sequenced by Sanger dideoxy sequencing. Based on
161 nucleotide BLAST searches (megablast, <https://blast.ncbi.nlm.nih.gov/Blast.cgi>), five belonged to
162 Cladophorales and the remaining five to diverse red algae observed at the sampling site (e.g.,
163 *Peyssonnelia* spp.). Four genetic variants of the cladophoralean species SSU rDNA were found
164 with 4 to 10 nucleotide differences. rDNA ITS and partial LSU rDNA were amplified (PCR
165 conditions as above) by using a specific forward primer for the cladophoralean species, 5'-
166 TGCGAAAGTGCATCGTGATG-3', and the ulvophyte reverse primer D2FL 5'-
167 GGTCCTGTTTCAAGACGG-3' (Leliaert et al. 2007a), purified, and Sanger-sequenced from
168 the primary PCR product (two polymorphic sites were identified). Sequences were deposited in
169 NCBI GenBank under the accessions KU359232-KU359236.

170 Sequences were added to updated phylogenetic datasets used previously (Leliaert et al.
171 2007a, 2009b; Table S2 in the Supporting Information), aligned in MAFFT v7.215 (Kato and
172 Standley 2013), and stripped of hypervariable sites in BMGE v1.1 (Criscuolo and Gribaldo 2010)
173 by using the -h 0.4 -g 0.35 parameters. Alignments were visually checked and concatenated in
174 Seaview v4.4.2, and are available from the Zenodo open access repository
175 <https://doi.org/10.5281/zenodo.5584487>. Maximum likelihood phylogenies were computed in IQ-
176 Tree v1.3.8 (Nguyen et al. 2015) under the GTR+G4+I model with 1000 ultrafast and 300
177 nonparametric bootstrap replicates. Bayesian phylogenies were computed in MrBayes v3.2.2
178 (Ronquist and Huelsenbeck 2003) by using the nst = 6, rates=invgamma, and ngammacat = 4
179 priors, 2 chains, and 25% burnin after convergence to stopval = 0.01.

180

181 **RESULTS**

182 *Phylogenetic analysis*

183 Maximum likelihood (ML) phylogenies from single gene datasets corresponding to the SSU
184 rDNA and the LSU rDNA moiety of the ITS/LSU fragment congruently placed the Southern Line
185 Island cladophoralean species (described hereunder as a new genus and species, *Brilliantia*
186 *kiribatiensis*) inside the Boodleaceae (*Chamaedoris* clade) of the Cladophorales as a sister taxon
187 to *Struvea elegans* (Fig. S1 in the Supporting Information). Concatenated ML and Bayesian
188 phylogenies based on SSU, ITS, and LSU in selected representatives (Table S2) were in line with
189 these results: *B. kiribatiensis* was unambiguously placed within the Boodleaceae, and specifically
190 affiliated with *Struvea elegans*, though with weak support (Fig. 2). *Struvea elegans* and the
191 Southern Line Island species formed a separate lineage from the *Struvea plumosa* clade
192 (containing the type of *Struvea*, *S. plumosa*), as reported previously (Leliaert et al. 2007, 2009).
193 Other genera in the clade, *Phyllodictyon*, *Apjohnia*, *Chamaedoris*, and *Boodlea* were
194 monophyletic and well separated from one another. No environmental sequences closely similar to
195 SSU and ITS/LSU rDNAs of *B. kiribatiensis* were found in environmental clone libraries in
196 GenBank.

197

198 *Morphological observations*

199 *Brilliantia kiribatiensis* formed bright green mats (Figs. 3, a-d, 4, a-d), up to 5 cm across,
200 composed of intertwined, irregularly branched rhizoids that were firmly attached to the
201 substratum, from which densely clustered, erect, unbranched, single-celled, wider diameter
202 filaments developed. Rhizoidal cells were 100-150 μm in diameter (Fig. 5, e-g). The upright
203 filaments were 2.5–6 cm high and 750-1100 μm in diameter (Figs. 3, e-f, 5, a-d). In some erect
204 cells, segregative cell division was observed at the distal end of the cell, in which the protoplast
205 divided into several, rounded or elongated daughter protoplasts, which subsequently formed new
206 cell walls, resulting in 5 to 6 cells of more or less equal length (Fig. 4c arrows, Fig. 6, a-e). In
207 some of these cells, cytoplasmic aggregation was observed (Fig. 6, c-f), as well as developing
208 crater-like pores in the cell wall (Fig. 6f, arrowhead). These cells can thus be interpreted as
209 zoosporangia or gametangia, which develop from vegetative cells following segregative cell
210 division, with pores through which the zoospores or gametes are released. Although we did not
211 observe release of zoids directly, some filaments were found with empty apical cells indicative of
212 zoid release (Fig. 4, d and e, arrowheads). Older empty cells were found to be degraded (Fig. 4f,

213 double arrowheads). Some other cells contracted their protoplasts into cytoplasmic spheres that
214 produced new cell walls, possibly in response to mechanical damage by collecting (Fig. 3f,
215 asterisks). Chloroplasts in the rhizoidal and upright cells contained a single pyrenoid, and formed
216 an open parietal reticulum (Fig. 6, g-h). No crystalline cell inclusions were observed.

217

218 *Habitat and geographical distribution.*

219 Specimens of *Brilliantia kiribatiensis* were found firmly attached to hard substratum primarily on
220 carbonate reef structures or dead coral skeletons. Other seaweeds found in these communities
221 include species of *Halimeda*, *Lobophora*, Peyssonneliaceae, abundant populations of several
222 genera of crustose coralline algae, and highly grazed and cropped mixed filamentous turf algal
223 communities. Abundance and distribution of *B. kiribatiensis* in the Southern Line Islands varied
224 (Fig. 1c), but the species was among the most common macroalgal taxa observed in subtidal
225 habitats from 5-25 m (Fig. S2 in the Supporting Information) on four of the five islands, Flint,
226 Vostok, Malden, and Millennium, with lower relative abundance in the algal community on
227 Starbuck probably as a result of the predominance of *Halimeda* spp. (Smith et al. 2016).
228 *Brilliantia kiribatiensis* may be more widely distributed throughout the Pacific as other sightings
229 were confirmed from neighboring islands, including Orona Atoll in the Phoenix Islands of Kiribati
230 in May 2018, and Rangiroa and Takapoto Atolls in the Tuamotus of French Polynesia in
231 September 2021 (Figs. 1b, 4).

232

233 *Taxonomic proposals.*

234 Based on the distinct phylogenetic position of the cladophoralean species from the Southern Line
235 Islands in the Boodleaceae (*Chamaedoris* clade sensu Leliaert et al. 2007) and the morphological
236 features that clearly distinguish it from other genera in that clade (*Apjohnia*, *Boodlea*,
237 *Chamaedoris*, *Cladophoropsis*, *Phyllodictyon*, *Struvea*; Table 1), we propose a new species and
238 genus in the Boodleaceae.

239

240 ***Brilliantia*** Leliaert, E.Kelly & Jen.E.Smith **gen. nov.**

241 *Diagnosis*: Genus of Boodleaceae distinguished from other genera in the family by rhizoidal mats
242 producing upright, unbranched, elongate, single-celled filaments, with zoidangia formed by
243 segregative cell division.

244 *Etymology*: Referring to the bright color of the thallus.

245 *Type species*. *B. kiribatiensis* Leliaert, E.Kelly & Jen.E.Smith

246

247 ***Brilliantia kiribatiensis*** Leliaert, E.Kelly & Jen.E.Smith **sp. nov.**

248 *Diagnosis*: Thallus forming bright green mats, up to 5 cm across, composed of irregularly
249 branched rhizoids and upright, unbranched, elongate, single-celled filaments, 2.5–6 cm high and
250 750–1100 µm in diameter. Segregative cell division in the upper part of the upright filaments
251 resulting in uniseriate rows of cells that transform into zoidangia.

252 *Etymology*: Referring to the Republic of Kiribati to which the Southern Line Islands (type locality)
253 belong.

254 *Holotype*: Republic of Kiribati, Southern Line Islands, Millennium, coral reef, 4 m deep, leeward
255 side of island, 09°57' S 150°13' W, 10 October 2013, leg. Emily Kelly SLI 035 (BISH 777505).

256 *Representative DNA sequences*: KU359234 (SSU ribosomal RNA gene), KU359236 (partial SSU
257 ribosomal RNA gene, internal transcribed spacer region, and partial LSU ribosomal RNA gene).
258 Sequences from a silica gel preserved specimen (labelled 'SP1' and housed in SCR) collected
259 from the type locality on 11 September 2013.

260 *Additional specimens examined (paratypes)*: Republic of Kiribati, Southern Line Islands,
261 Millennium, forereef on coral, 10 m deep, 09°57' S 150°13' W, 17 April 2009, leg. Jennifer E.
262 Smith 0148A (BISH 782311); Vostok, forereef on coral, 12 m deep, 10°03' S 152°18' W, 3 April
263 2009, leg. Jennifer E. Smith 0161B (BISH 782308); Vostok, coral reef, 10 m deep, leeward side of
264 island, 10°04' S 152°18' W, 23 October 2013, leg. Emily Kelly SLI 045 (SCR); Flint, coral reef, 4
265 m deep, leeward side of island, 11°26' S 151°48' W, 19 October 2013, leg. Emily Kelly SLI 042

266 A-E (BISH 782306); Malden, coral reef, 10 m deep, leeward side of island, 04°01' S 154°59' W,
267 02 November 2013, leg. Emily Kelly SLI 049 (SCR).

268 *Habitat and geographical distribution: Brilliantia kiribatiensis* is found subtidally at 5-25 m
269 depth, on hard substratum primarily on carbonate reef structures or dead coral skeletons, and is
270 currently known from the five Southern Line Islands Flint, Vostok, Starbuck, Malden, and
271 Millennium (Kiribati), Orona in the Phoenix Islands (Kiribati), and the Rangiroa and Takapoto
272 Atolls in the Tuamotus (French Polynesia).

273

274 **Discussion**

275 The new genus *Brilliantia* is represented by the single species *B. kiribatiensis*, which formed a
276 distinct clade within the Boodleaceae. Previous molecular phylogenetic studies have indicated that
277 most boodleacean genera as originally circumscribed, including *Boodlea*, *Chamaedoris*,
278 *Cladophoropsis*, *Phyllodictyon*, and *Struvea*, were non-monophyletic. A series of systematic
279 studies has aimed to revise the taxonomy of the group so that it better reflects evolutionary
280 relationships (Kooistra et al. 1993, Kraft and Wynne 1996, Leliaert and Coppejans 2007, Leliaert
281 et al. 2007b,c). A number of taxonomically problematic groups remain however, including the
282 *Boodlea* complex (including species of *Boodlea*, *Phyllodictyon*, *Cladophoropsis* and *Struveopsis*),
283 where traditional and phylogenetic species definitions are in complete disagreement with each
284 other due to a combination of cryptic diversity and intraspecific morphological variation (Leliaert
285 et al. 2009b).

286 Our phylogenetic analyses indicated that *Brilliantia kiribatiensis* is sister to *Struvea*
287 *elegans*, a species from the tropical Western Atlantic, typically growing in deeper waters, down to
288 40 m (Taylor 1960, Børgesen 1912, Littler and Littler 2000). The species has also been reported
289 from the Indian and Pacific Ocean (Guiry and Guiry 2021), although these records need
290 verification by DNA sequence data. *Struvea elegans* is characterized by delicate, erect, stipitate,
291 net-like blades, thus clearly differing from *B. kiribatiensis* which lacks such blades.

292 *Brilliantia* may be confused with juvenile, unbranched stages of *Struvea* species (Fig. 7).
293 However, during our surveys across all islands and different years and seasons no blade-like

294 structures were observed in any of the *B. kiribatiensis* populations, providing confidence that
295 branching is absent in this species, at least in situ. Moreover, the observation that reproductive
296 cells were formed in the apical part of the upright filaments ('stipes') indicates that these
297 morphological forms represent the full-grown stage of the species. Nevertheless, we cannot
298 exclude the possibility that *B. kiribatiensis* may take a different form in unexplored environments
299 such as mesophotic habitats, as has for example been shown in a species of *Caulerpa* (Sauvage et
300 al. 2021). *Brilliantia* is also morphologically clearly distinct from the other genera within the
301 family Boodleaceae (Table 1). It superficially resembles some coarse *Cladophoropsis* species,
302 such as *C. magna* or *C. philippinensis*, but can be clearly distinguished by the unbranched
303 filaments (Leliaert and Coppejans 2006). Thus the morphological distinctness and separate
304 phylogenetic position warrants the designation of a new species and genus.

305 Our phylogenetic analysis agrees with previous studies and indicates that *Struvea* is
306 currently paraphyletic, with the type of the genus (*S. plumosa*) grouping separately from *S.*
307 *elegans* and *Brilliantia kiribatiensis*. *Struvea elegans* may thus need to be transferred to another
308 genus, possibly *Brilliantia*. However, statistical support for the sister relationship between *S.*
309 *elegans* and *B. kiribatiensis* was low, so we prefer to await phylogenetic analyses with additional
310 taxon sampling (e.g., adding *S. elegans* samples from the Indian and Pacific Oceans) before
311 proposing formal taxonomic changes.

312 *Brilliantia* shares a specialized mode of cell division – segregative cell division – with
313 some other species of Cladophorales. In segregative cell division the protoplasm cleaves into
314 spherical portions, which later expand and develop into new cells. Segregative cell division is
315 fundamentally different from other cell division types in the green algae, both at the macroscopic
316 and ultrastructural levels (Okuda et al. 1997, Mine et al. 2008). In some genera, such as
317 *Siphonocladus* and *Struvea*, these cells remain inside the mother cell, expand and form new
318 vegetative branches (Kraft and Wynne 1996, Okuda et al. 2016), while in other taxa, such as
319 *Boergesenia* and *Valonia ventricosa*, the segregated cells are released from the degenerated
320 mother cell, settle and form new thalli (Olsen and West 1988). In *Brilliantia*, the new cells remain
321 in the parent cell, but do not form new lateral branches as in *Struvea*. Instead, some of these cells
322 transform into zoidangia. Reproduction by zoids is rarely observed in the Boodleaceae, but in
323 some species, including *Cladophoropsis membranacea*, *Phyllodictyon pulcherrimum*, and *Struvea*
324 *elegans*, cells in the terminal branch systems have been observed to transform into zoidangia with

325 lateral conical projections through which the zoids are released (Leliaert 2004), similar to the
326 structures observed in *B. kiribatiensis*.

327 The intensive grazing pressure by fish and sea urchins, which is typical in tropical shores,
328 has led to the evolution of a special mode of wounding reaction in some cladophoralean species,
329 which was also observed in *Brilliantia*. This reaction resembles segregative cell division where
330 after mechanical damage, cells rapidly contract and separate their cytoplasm into numerous
331 spherical protoplasts, which later secrete new cell walls and grow into new cells (La Claire 1982,
332 Mine et al. 2008). The whole process takes place in a couple of seconds. The cells either remain
333 within the mother cell or are released and develop into new thalli.

334 *Brilliantia kiribatiensis* is currently only known from the Southern Line Islands although
335 observations (without voucher specimens) suggest that it may also occur in the neighboring
336 Phoenix Islands (also in the Republic of Kiribati), as well as the Tuamotus of French Polynesia.
337 Given the vast number of islands and atolls that exist across the Pacific that have never had
338 thorough biodiversity assessments, *Brilliantia* could have a broader distribution than described
339 here. It is also possible that *Brilliantia* has been overlooked in other regions of the Indo-Pacific or
340 has been misidentified as young forms of other cladophoralean species; however, its striking
341 morphological appearance and conspicuous habit makes this unlikely. It is therefore reasonable to
342 assume that *B. kiribatiensis* has a relatively narrow geographical range, possibly restricted to the
343 remote central Pacific. Some other species of Boodleaceae have similarly restricted ranges,
344 including the mesophotic *Struvea gardineri* and *Phyllodictyon orientale*, only known from a few
345 Indian Ocean islands, including the Maldives, Seychelles, Cargados Carajos, and Socotra Island
346 (Leliaert and Coppejans 2007), *Struvea thoracica*, which has only been found in Queensland and
347 New Caledonia (Kraft and Millar 2005), and *Apjohnia laetevirens*, which is restricted to Southern
348 Australia and Tasmania (Womersley 1984). Conversely, other species in the family, mainly in the
349 *Boodlea* complex, have wider ranges, sometimes spanning different ocean basins, which has been
350 explained by the ability of these species to form free-floating thalli that facilitate long distance
351 dispersal (van den Hoek 1987, van der Strate et al. 2002, Leliaert et al. 2009b).

352 Based on significant overlap of marine species diversity, the Line Islands are considered
353 part of the larger Indo-Polynesian, or Eastern Indo-Pacific marine provinces (van den Hoek 1984,
354 Briggs and Bowen 2012, Kulbicki et al. 2014, Cowman et al. 2017). Within these larger regions,

355 the Line Islands have been variously allied biogeographically depending on the criteria or
356 taxonomic groups used for drawing biogeographic divisions (Stoddart 1992). In the scheme of
357 Spalding (2007), the Northern Line Islands, Malden, Starbuck are grouped with the Phoenix,
358 Tokelau, Northern Cook, and Samoa Islands in the Central Polynesia marine ecoregion, while the
359 three most southern Islands, Vostok, Millennium and Flint, are grouped in the Southeast Polynesia
360 marine ecoregion along with the Tuamotus, Pitcairn Islands, Southern Cook and Austral Islands,
361 and Society Islands (Fig. 1a). The geographical isolation of these oceanic island groups is reflected
362 in the relatively low marine biodiversity, especially compared with islands in the Central Indo-
363 Pacific (Cowman et al. 2017, Etti and Schils 2016).

364 The Central Polynesian islands have been characterized by high marine faunal endemism
365 (Cowman et al. 2017), but for marine macroalgae, endemism in the region has been less well
366 studied. Checklists from Samoa (Skelton and South 2004), the Phoenix islands (South et al. 2001),
367 Northern Line Islands (Tsuda et al. 2012), and other islands of Central Polynesia (Tsuda and
368 Walsh 2013) indicate that most seaweed species are widely distributed. Notable examples include
369 *Halimeda fragilis*, *Dictyopteris repens*, and *Antithamnionella breviramosa*, which are widely
370 recorded in the tropical Indo-Pacific, and *Bryopsis pennata*, *Antithamnion antillanum*, and
371 *Heterosiphonia crispella* with pantropical ranges. Other species, including *Ceramium krameri*,
372 *Chondria simpliciuscula*, *Corallophila kleiwegii*, *Cryptonemia yendoii*, *Dotyella hawaiiensis*,
373 *Herposiphonia pacifica*, *Polysiphonia homoia*, and *P. upolensis*, have narrower ranges within
374 Polynesia, consistent with the notion that macroalgal assemblages on Pacific Islands display
375 higher within-archipelago similarities than between-archipelago similarities (Schils et al. 2013,
376 Tsuda 2014). This biogeographical clustering indicates the importance of evolutionary processes
377 such as dispersal and speciation in seaweed biodiversity patterns, as has been illustrated by
378 molecular data in some red and brown seaweeds (Payo et al. 2013, Vieira et al. 2017, Leliaert et
379 al. 2018, Yip et al. 2020). These studies have also shown that a lot of diversity on remote oceanic
380 islands likely remains to be discovered, which has implications for our knowledge of
381 provincialism of seaweeds in the Pacific Ocean. Recently a number of new species of marine
382 macroalgae, restricted to Pacific islands, have been identified or described based on morphological
383 and DNA-sequence data (Vieira et al. 2014, Spalding et al. 2016, Gabriel et al. 2020, Sherwood et
384 al. 2020, Sherwood et al. 2021), including the red alga *Dissimularia withallii* from Jarvis Island,
385 Northern Line Islands (Kraft and Saunders 2014). The new genus and species *Brilliantia*

386 *kiribatiensis* adds to our knowledge of endemic species in the region.

387 The geographical origin of *Brilliantia kiribatiensis* is unclear (its candidate sister species,
388 *Struvea elegans*, has a tropical western Atlantic distribution). It is possible the species emerged by
389 founder speciation in a relative recent timeframe, corresponding to the age (ca. 8 Ma) of the Line
390 Islands (Neall and Trewick 2008) or alternatively *B. kiribatiensis* may have persisted in the
391 broader Pacific over a longer time frame as a metapopulation (Heads 2018), after which it became
392 geographically isolated. Additional sampling (possibly uncovering more closely related species to
393 *B. kiribatiensis*) will be needed to further elucidate the biogeographical history of the group.

394 Finally, the finding of a new, possibly endemic species and genus of green macroalgae in
395 the Southern Line Islands has consequences for marine conservation in these remote and pristine
396 reef ecosystems. Our findings confirm previous reports highlighting the uniqueness of these
397 ecosystems and their ability to support previously undescribed macroalgal diversity. Given the
398 paucity of scientific data from many remote, uninhabited islands across the central Pacific there is
399 likely much diversity yet to be discovered in this region. However, the potential impacts of global
400 change threaten these unique habitats and the species they support, underlining the need for more
401 research and for the protection of these as of yet pristine habitats. Several recent studies have
402 shown the dramatic impact of coral bleaching and the demise of *Acropora* colonies on reefs in the
403 central Pacific, including Kiribati, indicating that these reefs may be on the forefront of climate
404 change (Cannon et al. 2021). In light of this, the Kiribati government recognizes the threats and
405 benefits from this wealth of rich natural resources and has developed the Southern Line Island
406 Marine Protected Area (SLIMPA) Management Plan 2020-2024 and Regulations 2020, which
407 implies that the islands of Flint, Vostok, Starbuck, Malden, and Millennium will be a no-take
408 marine protected area, similar to the Phoenix Islands Protected Area (PIPA). These efforts
409 demonstrate Kiribati's commitment to protect these pristine ecosystems, and fulfill its obligations
410 towards the Convention on Biological Diversity (CBD, <https://www.cbd.int/>).

411

412 **ACKNOWLEDGEMENTS**

413 We would like to thank the captain and crew of the MV Hanse Explorer for their support on
414 expeditions in both 2009 and 2013. The National Geographic Society funded the 2009 Pristine

415 Seas expedition to the Southern Line Islands, and numerous private donors funded the 2013
416 Scripps Oceanography expedition. We would like to thank Dr. James Maragos and Dr. David
417 Obura for being dive buddies to JES in 2009. Dr. Forest Rohwer provided invaluable insight and
418 support with regard to sampling and molecular tools. We thank Adi Khen for the drawing of *B.*
419 *kiribatiensis*, Dr. Michael Guiry and Dr. William Woelkerling for advice on nomenclature, and
420 Barbara Kennedy of the Bishop Museum's Herbarium Pacificum for curating the voucher
421 specimens. We thank the three reviewers for their valuable comments. The work performed and
422 samples were collected under research permits from the Republic of Kiribati.

423

424 **Data availability statement**

425 DNA sequences were deposited in NCBI GenBank under accession numbers KU359232-
426 KU359236. Sequence alignments, and data from the photographic benthic surveys, and
427 morphological measurements are available as supplementary material, and on the Zenodo open
428 access repository <https://doi.org/10.5281/zenodo.5584487>.

429

430 **Author contributions**

431 **F. Leliaert**: Writing- original draft (lead); Investigation (equal). **E.L.A. Kelly**: Conceptualization
432 (equal); Investigation (equal); Writing- original draft (supporting). **J. Janouškovec**: Investigation
433 (equal); Writing- review & editing (supporting). **M.D. Fox**: Investigation (supporting); Writing-
434 review & editing (supporting). **M.D. Johnson**: Investigation (supporting); Writing- review &
435 editing (supporting). **F.M. Redfern**: Writing- review & editing (supporting). **T. Eria**: Writing-
436 review & editing (supporting). **A.F. Haas**: Conceptualization (supporting); Funding acquisition
437 (supporting); Writing- review & editing (supporting). **E. Sala**: Conceptualization
438 (supporting); Funding acquisition (supporting); Writing- review & editing (supporting). **S.A.**
439 **Sandin**: Conceptualization (supporting); Funding acquisition (supporting); Writing- review &
440 editing (supporting). **J.E. Smith**: Conceptualization (lead); Funding acquisition (lead); Writing-
441 review & editing (supporting).

442

444 **REFERENCES**

- 445 Barott, K. L., Caselle, J. E., Dinsdale, E. A., Friedlander, A. M., Maragos, J. E., Obura, D.,
446 Rohwer, F. L., Sandin, S. A., Smith, J. E. & Zgliczynski, B. 2010. The lagoon at
447 Caroline/Millennium Atoll, Republic of Kiribati: natural history of a nearly pristine
448 ecosystem. *PLoS ONE* 5:e10950.
- 449 Boedeker, C., Leliaert, F. & Zuccarello, G. C. 2016. Molecular phylogeny of the Cladophoraceae
450 (Cladophorales, Ulvophyceae), with the resurrection of *Acrocladus* Nägeli and *Willeella*
451 Børgesen, and the description of *Lurbica* gen. nov. and *Pseudorhizoclonium* gen. nov. *J.*
452 *Phycol.* 52:905-28.
- 453 Børgesen, F. 1912. Some Chlorophyceae from the Danish West Indies. II. *Bot. Tidsskr.* 32:241-73.
- 454 Braun, C., Smith, J. & Vroom, P. 2009. Examination of algal diversity and benthic community
455 structure at Palmyra Atoll, US Line Islands. *Proc. 11th Int. Coral Reef Symp., Ft.*
456 *Lauderdale.* pp. 865-69.
- 457 Briggs, J. C. & Bowen, B. W. 2012. A realignment of marine biogeographic provinces with
458 particular reference to fish distributions. *J. Biogeogr.* 39:12-30.
- 459 Cannon, S. E., Aram, E., Beiateuea, T., Kiareti, A., Peter, M. & Donner, S. D. 2021. Coral reefs in
460 the Gilbert Islands of Kiribati: Resistance, resilience, and recovery after more than a
461 decade of multiple stressors. *PLoS ONE* 16:e0255304.
- 462 Cowman, P. F., Parravicini, V., Kulbicki, M. & Floeter, S. R. 2017. The biogeography of tropical
463 reef fishes: endemism and provinciality through time. *Biol. Rev.* 92:2112-30.
- 464 Criscuolo, A. & Gribaldo, S. 2010. BMGE (Block Mapping and Gathering with Entropy): a new
465 software for selection of phylogenetic informative regions from multiple sequence
466 alignments. *BMC Evol. Biol.* 10:1-21.
- 467 Etti, R. & Schils, T. 2016. Global biogeography of marine algae with applications for coral reef
468 connectivity. *Proc. 13th Int. Coral Reef Symp., Honolulu.* pp. 28-47.
- 469 Fox, M. D., Williams, G. J., Johnson, M. D., Radice, V. Z., Zgliczynski, B. J., Kelly, E. L.,
470 Rohwer, F. L., Sandin, S. A. & Smith, J. E. 2018. Gradients in primary production predict
471 trophic strategies of mixotrophic corals across spatial scales. *Curr. Biol.* 28:3355-63. e4.
- 472 Gabriel, D., Draisma, S. G. A., Schils, T., Schmidt, W. E., Sauvage, T., Harris, D. J., Norris, J. N.
473 & Fredericq, S. 2020. Quite an oddity: new worldwide records of *Renouxia*
474 (Rhodogorgonales, Rhodophyta), including *R. marerubra* sp. nov. *Eur. J. Phycol.* 55:197-

- 475 206.
- 476 Guiry, M. D. & Guiry, G. M. 2021. AlgaeBase. World-wide electronic publication, National
477 University of Ireland, Galway. <https://www.algaebase.org>; searched on 24 Oct 2021.
- 478 Heads, M. 2018. Metapopulation vicariance explains old endemics on young volcanic islands.
479 *Cladistics* 34:292-311.
- 480 Huisman, J. M. & Leliaert, F. 2015. Cladophorales. In Huisman, J. M. [Ed.] *Marine benthic algae*
481 *of North-western Australia, 1: green and brown algae*. Australian Biological Resources
482 Study; CSIRO Publishing, pp. 32-67.
- 483 Johnson, M. D., Fox, M. D., Kelly, E. L., Zgliczynski, B. J., Sandin, S. A. & Smith, J. E. 2020.
484 Ecophysiology of coral reef primary producers across an upwelling gradient in the tropical
485 central Pacific. *PLoS ONE* 15:e0228448.
- 486 Johnston, E. T., Conklin, K. Y., Fredrick, P. & Sherwood, A. R. 2018. Pyrosequencing and
487 culturing of Hawaiian corticolous biofilms demonstrate high diversity and confirm
488 phylogenetic placement of the green alga *Spongiochrysis hawaiiensis* in Cladophorales
489 (Ulvophyceae). *Phycologia* 57:572-80.
- 490 Katoh, K. & Standley, D. M. 2013. MAFFT multiple sequence alignment software version 7:
491 improvements in performance and usability. *Mol. Biol. Evol.* 30:772-80.
- 492 Kerr, V. & Wragg, G. 2008. Southern Line Islands - Observations and Marine Survey Report 2008
493 (online publication,
494 [https://www.researchgate.net/publication/242330400_Southern_Line_Islands_-](https://www.researchgate.net/publication/242330400_Southern_Line_Islands_-_Observations_and_Marine_Survey_Report_2008)
495 [Observations_and_Marine_Survey_Report_2008](https://www.researchgate.net/publication/242330400_Southern_Line_Islands_-_Observations_and_Marine_Survey_Report_2008), accessed on 24 Oct 2021).
- 496 Kooistra, W. H. C. F., Olsen, J. L., Stam, W. T. & van den Hoek, C. 1993. Problems relating to
497 species sampling in phylogenetic studies: an example of non-monophyly in
498 *Cladophoropsis* and *Struvea* (Siphonocladales, Chlorophyta). *Phycologia* 32:419-28.
- 499 Kraft, G. T. & Millar, A. J. K. 2005. *Struvea thoracica* sp. nov. (Cladophorophyceae), a new deep-
500 water chlorophyte from the Great Barrier Reef and New Caledonia. *Phycologia* 44:305-11.
- 501 Kraft, G. T. & Saunders, G. W. 2014. *Crebradomus* and *Dissimularia*, new genera in the family
502 Chondrymeniaceae (Gigartinales, Rhodophyta) from the central, southern and western
503 Pacific Ocean. *Phycologia* 53:146-66.
- 504 Kraft, G. T. & Wynne, M. J. 1996. Delineation of the genera *Struvea* Sonder and *Phyllodictyon*
505 J.E. Gray (Cladophorales, Chlorophyta). *Phycol. Res.* 44:129-43.
- 506 Kulbicki, M., Parravicini, V., Bellwood, D. R., Arias-González, E., Chabanet, P., Floeter, S. R.,

- 507 Friedlander, A., McPherson, J., Myers, R. E., Vigliola, L. & Mouillot, D. 2014. Global
508 biogeography of reef fishes: A hierarchical quantitative delineation of regions. *PLoS ONE*
509 8:e81847.
- 510 La Claire, J. W. 1982. Cytomorphological aspects of wound healing in selected Siphonocladales
511 (Chlorophyceae). *J. Phycol.* 18:379-84.
- 512 Leliaert, F. 2004. *Taxonomic and phylogenetic studies in the Cladophorophyceae (Chlorophyta)*.
513 PhD, Ghent University, 294 pp.
- 514 Leliaert, F. & Coppejans, E. 2004. Crystalline cell inclusions: a new diagnostic character in the
515 Cladophorophyceae (Chlorophyta). *Phycologia* 43:189-203.
- 516 Leliaert, F. & Coppejans, E. 2006. A revision of *Cladophoropsis* Børgesen (Siphonocladales,
517 Chlorophyta). *Phycologia* 45:657-79.
- 518 Leliaert, F. & Coppejans, E. 2007. Systematics of two deep-water species from the Indo-West
519 Pacific: *Struvea gardineri* A.Gepp & E.Gepp and *Phyllodictyon orientale* (A.Gepp &
520 E.Gepp) Kraft & M.J.Wynne (Siphonocladales, Chlorophyta). *Bot. J. Linn. Soc.* 153:115-
521 32.
- 522 Leliaert, F., De Clerck, O., Verbruggen, H., Boedeker, C. & Coppejans, E. 2007a. Molecular
523 phylogeny of the Siphonocladales (Chlorophyta: Cladophorophyceae). *Mol. Phylogenet.*
524 *Evol.* 44:1237-56.
- 525 Leliaert, F., Huisman, J. M. & Coppejans, E. 2007b. Phylogenetic position of *Boodlea vanbosseae*
526 (Siphonocladales, Chlorophyta). *Cryptogam. Algal.* 28:337-51.
- 527 Leliaert, F., Millar, A. J. K., Vlaeminck, C. & Coppejans, E. 2007c. Systematics of the green
528 macroalgal genus *Chamaedoris* Montagne (Siphonocladales), with an emended description
529 of the genus *Struvea* Sonder. *Phycologia* 46:709-25.
- 530 Leliaert, F., Payo, D. A., Gurgel, C. F. D., Schils, T., Draisma, S. G. A., Saunders, G. W., Kamiya,
531 M., Sherwood, A. R., Lin, S. M., Huisman, John M., Le Gall, L., Anderson, R. J., Bolton,
532 John J., Mattio, L., Zubia, M., Spokes, T., Vieira, C., Payri, C. E., Coppejans, E., D'hondt,
533 S., Verbruggen, H. & De Clerck, O. 2018. Patterns and drivers of species diversity in the
534 Indo-Pacific red seaweed *Portieria*. *J. Biogeogr.* 45:2299-313.
- 535 Leliaert, F., Rueness, J., Boedeker, C., Maggs, C. A., Cocquyt, E., Verbruggen, H. & De Clerck,
536 O. 2009a. Systematics of the marine microfilamentous green algae *Uronema curvatum* and
537 *Urospora microscopica* (Chlorophyta). *Eur. J. Phycol.* 44:487-96.
- 538 Leliaert, F., Verbruggen, H., Wysor, B. & De Clerck, O. 2009b. DNA taxonomy in

- 539 morphologically plastic taxa: algorithmic species delimitation in the *Boodlea* complex
540 (Chlorophyta: Cladophorales). *Mol. Phylogenet. Evol.* 53:122-33.
- 541 Leliaert, F., Wysor, B., Verbruggen, H., Vlaeminck, C. & De Clerck, O. 2008. *Phyllocladion*
542 *robustum* (Setchell et Gardner) comb. nov. (Siphonocladales, Chlorophyta), a
543 morphologically variable species from the tropical Pacific coast of America. *Cryptogam.*
544 *Algol.* 29:217-33.
- 545 Littler, D. S. & Littler, M. M. 2000. *Caribbean reef plants: an identification guide to the reef*
546 *plants of the Caribbean, Bahamas, Florida and Gulf of Mexico*. Offshore Graphics,
547 Washington, 542 pp.
- 548 Mangubhai, S., Lovell, E., Abeta, R., Donner, S., Redfern, F. M., O'Brien, M., Aram, K. T.,
549 Gillett, R., Rotjan, R., Eria, T., Teetu, S. B. & Bebe, R. 2019. Kiribati: Atolls and marine
550 ecosystems (Chapter 37). In Sheppard, C. [Ed.] *World Seas: an Environmental Evaluation*
551 *(Second Edition)*. Academic Press, pp. 807-26.
- 552 McNaughton, E. E. & Goff, L. J. 1990. The role of microtubules in establishing nuclear spatial
553 patterns in multinucleate green algae. *Protoplasma* 157:19-37.
- 554 Medlin, L., Elwood, H. J., Stickel, S. & Sogin, M. L. 1988. The characterization of enzymatically
555 amplified eukaryotic 16S-like rRNA-coding regions. *Gene* 71:491-99.
- 556 Mine, I., Menzel, D. & Okuda, K. 2008. Morphogenesis in giant-celled algae. *Int. Rev. Cell Mol.*
557 *Biol.* 266:37-83.
- 558 Neall, V. E. & Trewick, S. A. 2008. The age and origin of the Pacific islands: a geological
559 overview. *Phil. Trans. R. Soc. B* 363:3293-308.
- 560 Nguyen, L. T., Schmidt, H. A., von Haeseler, A. & Minh, B. Q. 2015. IQ-TREE: A fast and
561 effective stochastic algorithm for estimating maximum-likelihood phylogenies. *Mol. Biol.*
562 *Evol.* 32:268-74.
- 563 Okuda, K., Mine, I., Morinaga, T. & Kuwaki, N. 1997. Cytomorphogenesis in cenocytic green
564 algae. V. Segregative cell division and cortical microtubules in *Dictyosphaeria cavernosa*
565 (Siphonocladales, Chlorophyceae). *Phycol. Res.* 45:189-96.
- 566 Okuda, K., Sekida, S., Hasebe, A., Iwabuchi, M., Kamiya, M. & Hishinuma, T. 2016. Segregative
567 cell division and the cytoskeleton in two species of the genus *Struvea* (Cladophorales,
568 Ulvophyceae, Chlorophyta). *Phycol. Res.* 64:219-29.
- 569 Olsen, J. L. & West, J. A. 1988. *Ventricaria* (Siphonocladales-Cladophorales complex,
570 Chlorophyta), a new genus for *Valonia ventricosa*. *Phycologia* 27:103-08.

- 571 Payo, D. A., Leliaert, F., Verbruggen, H., D'Hondt, S., Calumpong, H. P. & De Clerck, O. 2013.
572 Extensive cryptic species diversity and fine-scale endemism in the marine red alga
573 *Portieria* in the Philippines. *Proc. R. Soc. B* 280:20122660.
- 574 Ronquist, F. & Huelsenbeck, J. P. 2003. MrBayes 3: Bayesian phylogenetic inference under mixed
575 models. *Bioinformatics* 19:1572-74.
- 576 Sandin, S. & Charles, C. 2009. Line Islands. In Gillespie, R. & Clague, D. [Eds.] *Encyclopedia of*
577 *Islands*. University of California Press, pp. 553-58.
- 578 Sandin, S. A., Smith, J. E., DeMartini, E. E., Dinsdale, E. A., Donner, S. D., Friedlander, A. M.,
579 Konotchick, T., Malay, M., Maragos, J. E., Obura, D., Pantos, O., Paulay, G., Richie, M.,
580 Rohwer, F., Schroeder, R. E., Walsh, S., Jackson, J. B. C., Knowlton, N. & Sala, E. 2008.
581 Baselines and degradation of coral reefs in the Northern Line Islands. *PLoS ONE* 3:e1548.
- 582 Sauvage, T., Wynne, M. J., Draisma, S. G., Ortegón-Aznar, I., Mateo-Cid, L. E., Mendoza-
583 González, A. C., Martínez-Daranas, B. & Fredericq, S. 2021. *Caulerpa wysorii* sp. nov., a
584 denuded *Caulerpa* (Chlorophyta) resembling *C. sertularioides* when 'dressed'. *Phycologia*
585 60:107-19.
- 586 Schils, T., Vroom, P. S. & Tribollet, A. D. 2013. Geographical partitioning of marine macrophyte
587 assemblages in the tropical Pacific: a result of local and regional diversity processes. *J.*
588 *Biogeogr.* 40:1266-77.
- 589 Sherwood, A. R., Lin, S.-M., Wade, R. M., Spalding, H. L., Smith, C. M. & Kosaki, R. K. 2020.
590 Characterization of *Martensia* (Delesseriaceae; Rhodophyta) from shallow and mesophotic
591 habitats in the Hawaiian Islands: description of four new species. *Eur. J. Phycol.* 55:172-
592 85.
- 593 Sherwood, A. R., Paiano, M. O., Cabrera, F. P., Spalding, H. L., Hauk, B. B. & Kosaki, R. K.
594 2021. *Ethelia hawaiiensis* (Etheliaceae, Rhodophyta), a new mesophotic marine alga from
595 Manawai (Pearl and Hermes Atoll), Papahānaumokuākea Marine National Monument,
596 Hawai'i. *Pac. Sci.* 75:237-46.
- 597 Škaloud, P., Rindi, F., Boedeker, C. & Leliaert, F. 2018. *Freshwater Flora of Central Europe, Vol*
598 *13: Chlorophyta: Ulvophyceae*. Springer Spektrum, Berlin, Heidelberg, 288 pp.
- 599 Skelton, P. A. & South, G. R. 2004. New records and notes on marine benthic algae of American
600 Samoa - Chlorophyta & Phaeophyta. *Cryptogam. Algol.* 25:291-312.
- 601 Smith, J. E., Brainard, R., Carter, A., Grillo, S., Edwards, C., Harris, J., Lewis, L., Obura, D.,
602 Rohwer, F., Sala, E., Vroom, P. S. & Sandin, S. 2016. Re-evaluating the health of coral

- 603 reef communities: baselines and evidence for human impacts across the central Pacific.
604 *Proc. R. Soc. B* 283:20151985.
- 605 South, G., Skelton, P. & Yoshinaga, A. 2001. Subtidal benthic marine algae of the Phoenix
606 Islands, Republic of Kiribati, central Pacific. *Bot. Mar.* 44:559-70.
- 607 Spalding, H. L., Conklin, K. Y., Smith, C. M., O'Kelly, C. J. & Sherwood, A. R. 2016. New
608 Ulvaceae (Ulvophyceae, Chlorophyta) from mesophotic ecosystems across the Hawaiian
609 Archipelago. *J. Phycol.* 52:40-53.
- 610 Stoddart, D. R. 1992. Biogeography of the tropical Pacific. *Pac. Sci.* 46:276-93.
- 611 Taylor, W. R. 1960. *Marine algae of the eastern tropical and subtropical coasts of the Americas.*
612 University of Michigan Press, Ann Arbor, MI, 870 pp.
- 613 Tikhonenkov, D. V., Janouškovec, J., Keeling, P. J. & Mylnikov, A. P. 2016. The morphology,
614 ultrastructure and SSU rRNA gene sequence of a new freshwater flagellate, *Neobodo*
615 *borokensis* n. sp. (Kinetoplastea, Excavata). *J. Eukaryot. Microbiol.* 63:220-32.
- 616 Tsuda, R. 2014. Endemism of marine algae in the Hawaiian Islands. *Bishop Mus. Occas. Pap.*
617 115:23-27.
- 618 Tsuda, R. T., Fisher, J. R. & Vroom, P. S. 2012. Floristic account of the marine benthic algae from
619 Jarvis Island and Kingman Reef, Line islands, Central Pacific. *Micronesica* 43:14-50.
- 620 Tsuda, R. T. & Walsh, S. K. 2013. Bibliographic checklist of the marine benthic algae of Central
621 Polynesia in the Pacific Ocean (excluding Hawai'i and French Polynesia). *Micronesica*
622 2:1-91.
- 623 van den Hoek, C. 1984. World-wide latitudinal and longitudinal seaweed distribution patterns and
624 their possible causes, as illustrated by the distribution of rhodophytan genera. *Helgol.*
625 *Meeresunters.* 38:227-57.
- 626 van den Hoek, C. 1987. The possible significance of long-range dispersal for the biogeography of
627 seaweeds. *Helgol. Meeresunters.* 41:261.
- 628 van der Strate, H. J., Boele-Bos, S. A., Olsen, J. L., van de Zande, L. & Stam, W. T. 2002.
629 Phylogeographic studies in the tropical seaweed *Cladophoropsis membranacea*
630 (Chlorophyta, Ulvophyceae) reveal a cryptic species complex. *J. Phycol.* 38:572-82.
- 631 Vieira, C., Camacho, O., Sun, Z., Fredericq, S., Leliaert, F., Payri, C. & De Clerck, O. 2017.
632 Historical biogeography of the highly diverse brown seaweed *Lobophora* (Dictyotales,
633 Phaeophyceae). *Mol. Phylogenet. Evol.* 110:81-92.
- 634 Vieira, C., D'hondt, S., De Clerck, O. & Payri, C. E. 2014. Toward an inordinate fondness for

- 635 stars, beetles and *Lobophora*? Species diversity of the genus *Lobophora* (Dictyotales,
636 Phaeophyceae) in New Caledonia. *J. Phycol.* 50:1101-19.
- 637 Womersley, H. B. S. 1984. *The Marine Benthic Flora of Southern Australia. Part I.* Government
638 Printer, South Australia, Adelaide, 329 pp.
- 639 Yip, Z. T., Quek, R. Z. & Huang, D. 2020. Historical biogeography of the widespread macroalga
640 *Sargassum* (Fucales, Phaeophyceae). *J. Phycol.* 56:300-9.

641

Table 1. Morphological comparison of *Brilliantia* with the other genera of Boodleaceae

	<i>Apjohnia</i>	<i>Boodlea</i>	<i>Chamaedoris</i>	<i>Cladophoropsis</i>	<i>Phyllodictyon</i>	<i>Struvea</i>	<i>Brilliantia</i>
Habit	Erect, robust, stipitate capitula composed of a whorl or cluster of branches	Netlike cushions or blades, composed of densely branched filaments	Erect, robust, stipitate capitula, composed of whorls of branched filaments	Mats or cushions composed of long, irregularly branched cells; attached by rhizoids or tenacular cells	Erect, delicate, stipitate blades, composed of regularly branched filaments	Erect, delicate, stipitate blades or capitula, composed of regularly branched filaments	Filamentous mat and erect unbranched filaments
Stipe	Prominent, single-celled, unbranched, with annular constrictions near base	Absent or inconspicuous, with or without annular constrictions	Prominent, single-celled, unbranched, with annular constrictions over the entire length	Absent or inconspicuous	Prominent, unbranched or branched, with or without annular constrictions.	Prominent, generally single-celled and unbranched, with or without annular constrictions.	Erect filament regarded as homologues to the stipe in the other genera
Thallus reinforcement	Older cells of the capitulum producing hapteroid cells at	Cells connecting by tenacular cells	Entangling of capitulum filaments and cells connecting by	Entangling of filaments or cells connecting by tenacular cells	Cells connecting by tenacular cells at the apical or basal poles of	Cells connecting by tenacular cells at the apical poles of cells.	Tenacular cells absent

	their base		tenacular cells		cells.		
Mode of cell division	Centripetal wall ingrowths	Centripetal wall ingrowths	Centripetal wall ingrowths (capitulum filaments) and segregative cell division (distal end of stipe cell)	Centripetal wall ingrowths. Protoplasts formation (resembling segregative cell division) may occur as a wounding response.	Centripetal wall ingrowths	Segregative cell division or centripetal wall ingrowths	Segregative cell division
Crystalline cell inclusions (Leliaert and Coppejans 2004)	Elongate rod-shaped calcium oxalate (CaOx) crystals	Elongate prismatic CaOx crystals	Elongate prismatic or diamond shaped CaOx crystals (some species), Tetrahedral protein crystals (some species)	Elongate prismatic CaOx crystals	Diamond-shaped or hexagonal CaOx crystals	Diamond-shaped or hexagonal CaOx crystals (absent in <i>S. elegans</i>)	Absent

Habitat	Deep intertidal pools or subtidal	Intertidal or shallow subtidal	Intertidal or subtidal	Intertidal or subtidal	Generally subtidal	Intertidal or subtidal	Generally subtidal
Geographical distribution	Australia, New Caledonia, Norfolk Island	Global (sub)tropical	Global (sub)tropical	Global (sub)tropical	Global (sub)tropical	Global (sub)tropical	Southern Line Islands
Number of species	2	c. 10	3	c. 8	c. 7	5	1
Taxonomic notes		Included in the <i>Boodlea</i> complex		Non-monophyletic genus; <i>C. membranacea</i> (lectotype) included in the <i>Boodlea</i> complex. Other species (e.g. <i>C. herpestica</i>) are now placed in <i>Lychaete</i> .	Non-monophyletic genus; some species, e.g. <i>P. anastomosans</i> , included in the <i>Boodlea</i> complex.	Non-monophyletic genus; <i>S. elegans</i> with separate phylogenetic position	
References	(Womersley 1984)	(Leliaert et al. 2009b)	(Leliaert et al. 2007c)	(Leliaert and Coppejans 2006, Leliaert et al. 2009b, Boedeker et al. 2016)	(Leliaert and Coppejans 2007, Leliaert et al. 2008)	(Kraft and Wynne 1996, Leliaert et al. 2007c, Okuda et al. 2016)	This study

Fig. 1. Geographical location of the Southern Line Islands with indication of marine provinces (different colors) and ecoregions as defined in Spalding et al. (2007) (a); islands where *Brilliantia kiribatiensis* was recorded (b); and sampling and monitoring sites of the five Southern Line Islands with average percent cover of *B. kiribatiensis* (green circles) (c) (data available in Table S1).

Fig. 2. Maximum likelihood tree of the Boodleaceae (*Chamaedoris* clade) inferred from the concatenated SSU+ITS+LSU rDNA dataset, showing the phylogenetic position of *Brilliantia kiribatiensis*. Clades in the *Boodlea* complex (Leliaert et al. 2009b) include various morphological forms that are traditionally regarded as different species and genera, including *Boodlea* spp. (clades 1, 7, 9, 10), *Cladophoropsis* spp. (clades 1, 5, 10, 11, 13), and *Phyllodictyon anastomosans* (clades 1, 7, 8, 10). ML (IQ-Tree) ultrafast bootstrap / nonparametric bootstrap / and MrBayes posterior probabilities are shown at branches. Black dots on branches indicate full support in all three analyses.

Fig. 3. *Brilliantia kiribatiensis* from the Southern Line Islands. In situ photographs from Millennium Atoll, showing bright green tufts of densely clustered filaments, growing on carbonate reef structures or dead coral skeletons (a-d), and details of fresh samples showing the irregularly branched rhizoids from which erect, unbranched, single-celled filaments develop (e-f). Arrows indicate filaments that have undergone segregative cell division, resulting in 5 to 6 cells of more or less equal length. Asterisks (*) indicate contracted protoplasts, likely as a response to mechanical damage by collecting. Scale bars = 1 cm (e, f).

Fig. 4. *Brilliantia kiribatiensis* from Orona Atoll, Phoenix Islands (a-c), and Rangiroa (d) and Takapoto (e, f), Tuamotus. In situ photographs, showing tufts of densely clustered filaments, growing on carbonate reef structures. Arrows (c) indicate filaments that are undergoing segregative cell division. Arrowheads (d, e) indicate empty cells in the upper part of the filaments, possibly after release of zooids. Double arrowheads (f) indicate filaments in which the cell walls of empty cells are degraded.

Fig. 5. *Brilliantia kiribatiensis*. Upright, single-celled filaments developing rhizoids in the middle and basal parts of the cell (a, b). Apical part of filaments (c), with chloroplast layer visible underneath the cell wall (d). Intertwining rhizoids (e), anastomosing by hapteroid protrusions (f, g). Drawing by Adi Khen. Scale bars = 5 mm (a, b), 2 mm (c, e), 200 μ m (d), 100 μ m (f, g).

Fig. 6. *Brilliantia kiribatiensis*. Segregative cell division, in which the protoplast in the distal end of the cell divides into several, rounded or elongated daughter protoplasts, which subsequently form new cell walls, resulting in 5 to 6 cells of more or less equal length (a-e). Cytoplasmic aggregation observed in some cells after segregative cell division (c-f), with some cells developing crater-like pores in the cell wall (Fig. 6f, arrowhead). Chloroplasts with a single pyrenoid, forming closed to open parietal reticulum (g, h). Scale bars = 2 mm (a, c, d), 1 mm (b, e), 200 μm (f), 10 μm (g), 50 μm (h).

Fig. 7. Schematic representation of the developmental stages of *Struvea* species (A-E) and *Brilliantia kiribatiensis* (A-B). A. Young thallus consisting of a single-celled stipe; B. Segregative cell division in the distal end of the stipe cell resulting in a uniseriate row of cells (later becoming the central axis in *Struvea*); C. Each cell producing a pair of equally developing opposite lateral branches which elongate and form the primary branch systems of the blade; D-E. Segregative cell division and formation of lateral branches repeated in the primary laterals and apical cell of the central axis. In some *Struvea* species, this process is repeated, resulting in branch systems up to the 4th or even 5th order.

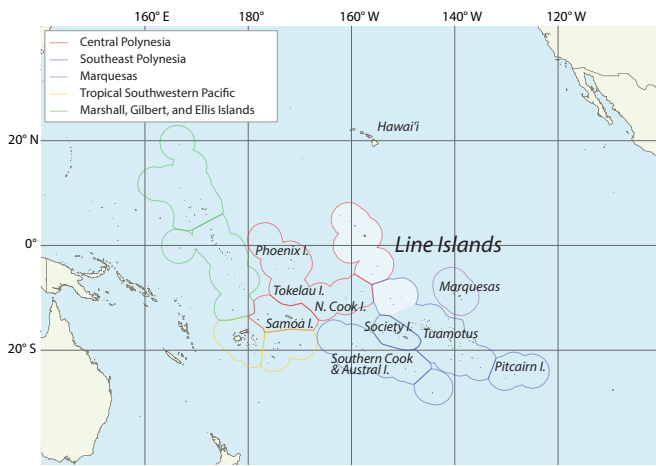
Fig. S1. Phylogeny of the Boodleaceae based on SSU (A) and LSU rDNA (B) single gene datasets. The Maximum Likelihood tree (IQ-Tree) is shown with ultrafast bootstrap supports at branches (>50 are shown). Each species name is followed by the isolate name, sequence accession, and site of isolation, separated by underscores, where available.

Fig. S2. Average percent cover of algae in the different island sites. Algal groups are identified to genus level for fleshy macroalgae or functional group for turf algae, branched red algae, crustose coralline algae, and cyanobacteria. Location of the sites is shown in Figure 1c. Data are available in Table S1.

Table S1. Percent cover of different algal groups in 1 m² photoquadrats. Algal groups are identified to genus level for fleshy macroalgae or functional group for turf algae, branched red algae, crustose coralline algae, and cyanobacteria.

Table S2. GenBank accessions, sample isolate codes and sites of collection for sequences included in the concatenated phylogenetic data set in Figure 2

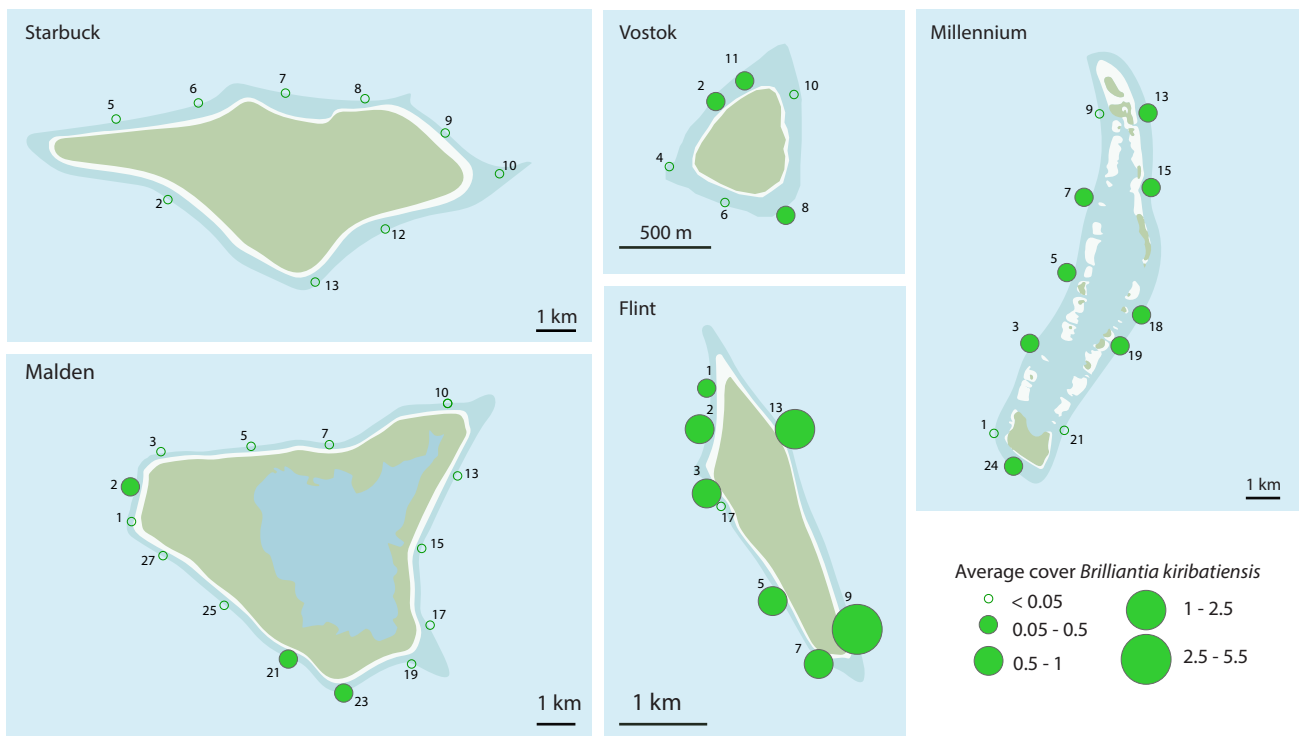
a

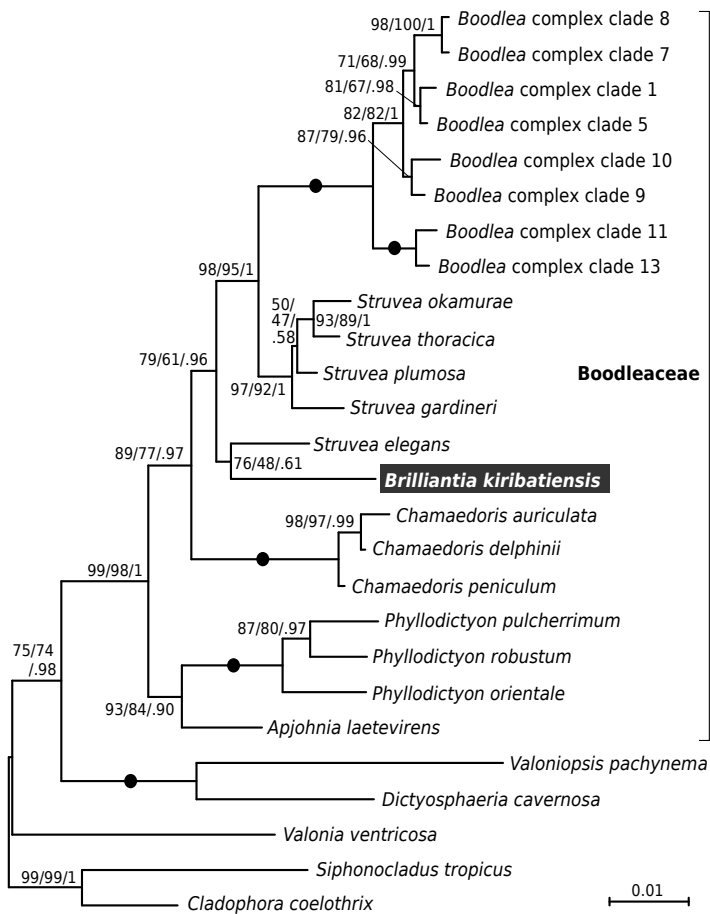


b



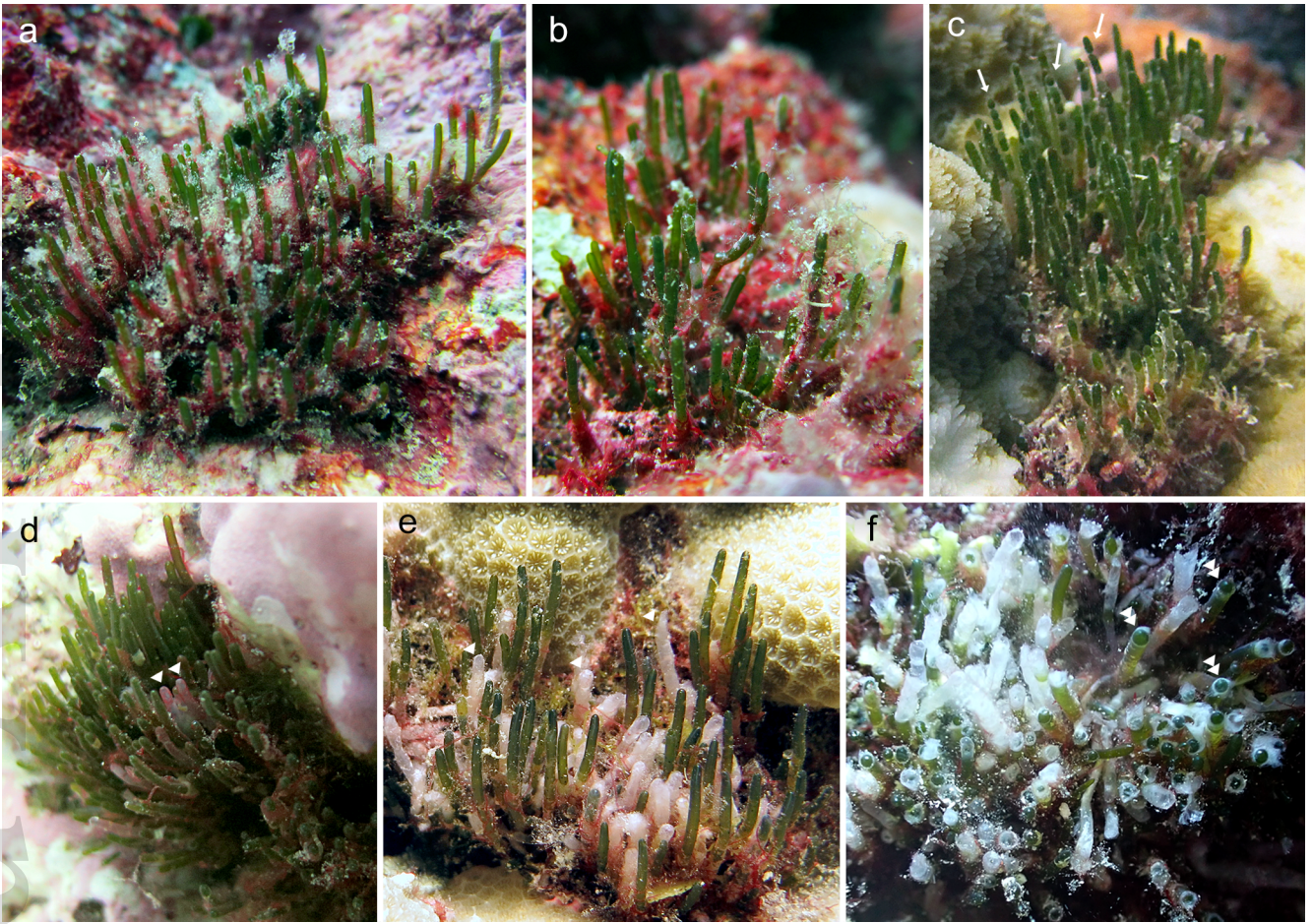
c



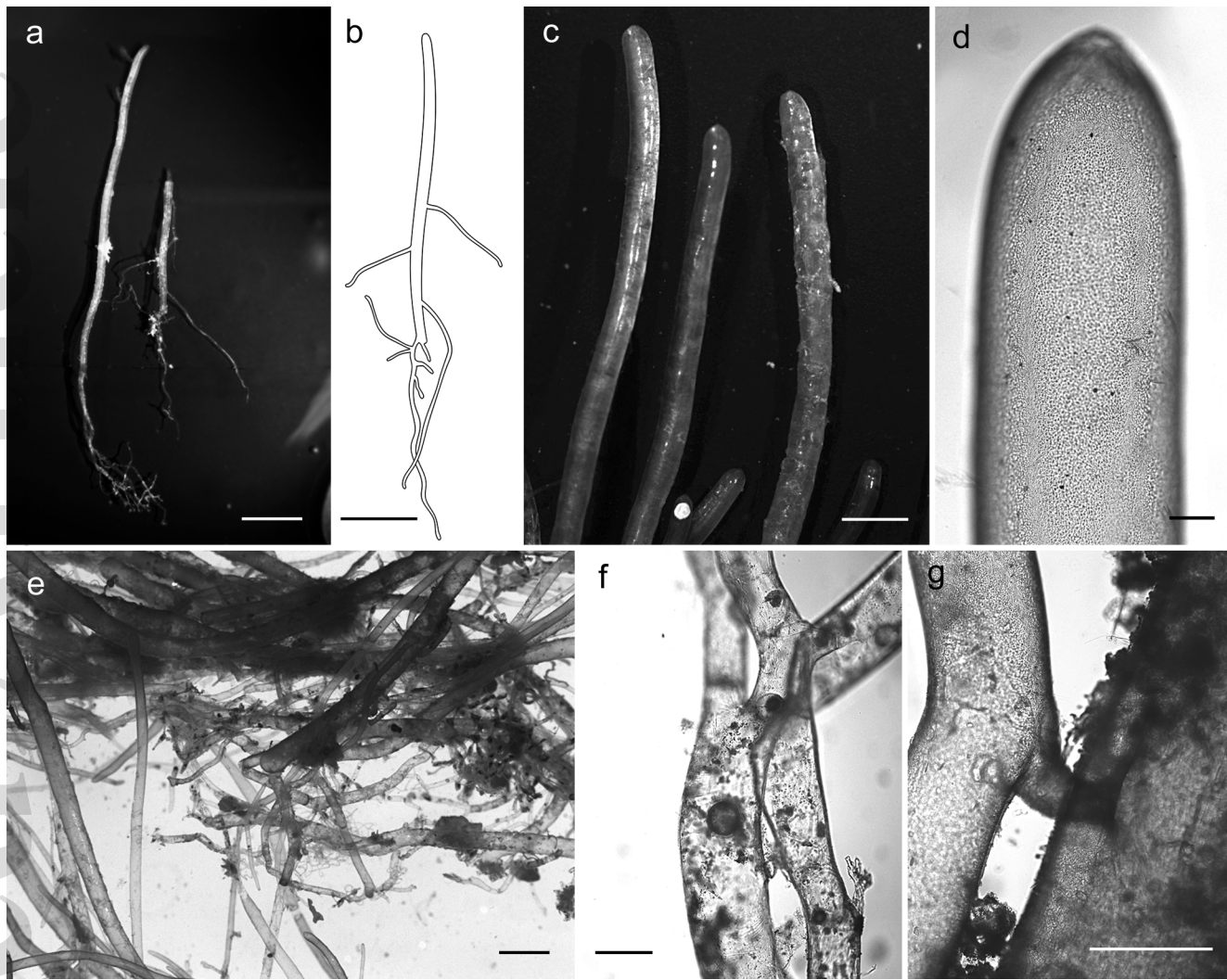




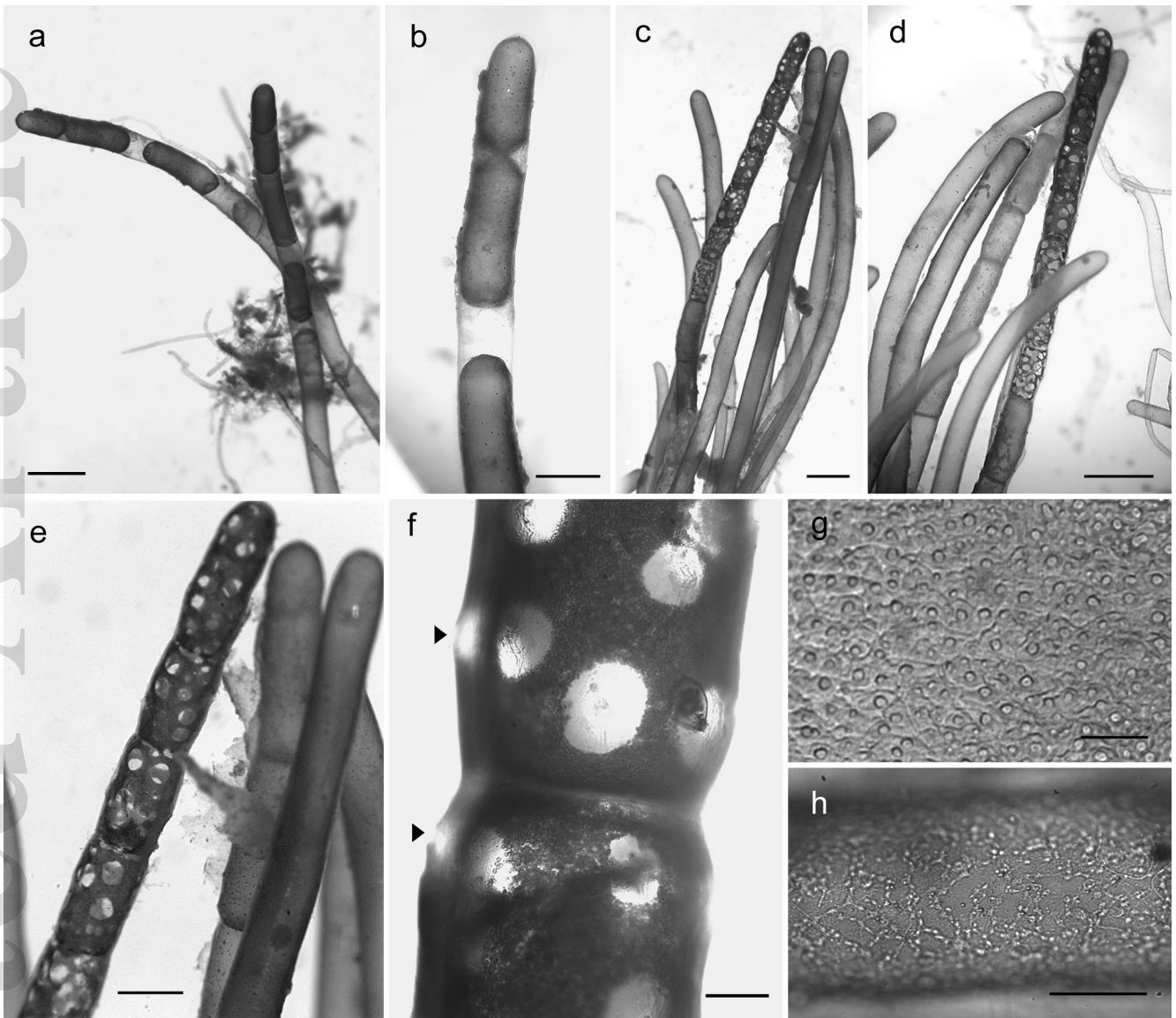
jpy_13230_f3.tif



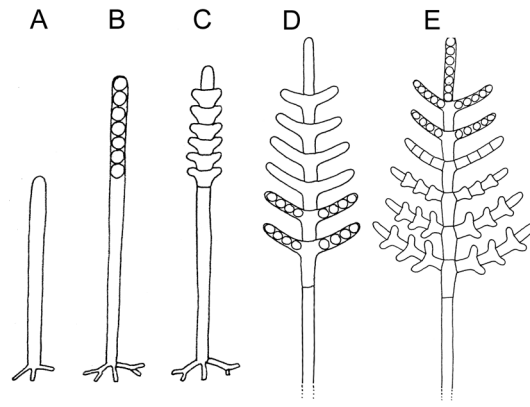
jpy_13230_f4.tif



jpy_13230_f5.tif



jpy_13230_f6.tif



jpy_13230_f7.tif