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# One hundred years later, resurrection of *Tydemanina gardineri* A. Gepp & E. Gepp (Udoteaceae, Chlorophyta) based on molecular and morphological data

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1 **ONE HUNDRED YEARS LATER, RESURRECTION OF *TYDEMANIA***  
2 ***GARDINERI* A. GEPP & E. GEPP (UDOTEACEAE, CHLOROPHYTA) BASED**  
3 **ON MOLECULAR AND MORPHOLOGICAL DATA**

4

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6

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14 **ABSTRACT**

15 *Tydemania* Weber-van Bosse is a genus belonging to the Udoteaceae family  
16 (Bryopsidales, Chlorophyta) and currently thought to be monospecific throughout its  
17 distribution range in the Indo-Pacific. We tested the assumption that *Tydemania* is a  
18 single species using species delimitation methods, morphological observations, and  
19 phylogenetic reconstructions of large datasets. Our molecular and morphological data  
20 recovered two distinct groups, which we argue are the type species *T. expeditionis*  
21 Weber-van Bosse and *T. gardineri* A. Gepp & E. Gepp. The latter is currently  
22 considered a synonym of the former and we resurrect this name from synonymy.  
23 *Tydemania gardineri* is distinguished morphologically from *T. expeditionis* by the  
24 systematic absence of glomeruli, whereas *T. expeditionis* can have glomeruli and  
25 flabella, glomeruli alone, or flabella alone. The two species can also be distinguished by  
26 the shape and length of the stalks at the basis of the flabella, the diameter of the main  
27 axis, and of the flabella siphons at the apices. In addition, they have different  
28 geographical distributions, with *T. gardineri* restricted to the Western Indian Ocean, and  
29 *T. expeditionis* extending from the Red sea, throughout the Indian Ocean and into the  
30 West-Pacific, including the coral triangle, the Philippines and Japan. From our dataset  
31 and literature search, we hypothesize its south-western distribution limit is in northern  
32 Madagascar. Finally, we confirm the synonymization of *T. mabahithae* with *T.*  
33 *expeditionis* based on specimens from the type-locality of the former ranging within the  
34 *T. expeditionis* species and we do retrieved thalli without flabella in several other  
35 specimens of *T. expeditionis*.

36 Keywords: macroalgae; Bryopsidales; species delimitation; phylogeny; molecular data;  
37 morphology; Indo-Pacific.

## 38 INTRODUCTION

39 *Tydemania* Weber-van Bosse is a genus of calcified siphonous green algae in the family  
40 Udoteaceae (Bryopsidales, Chlorophyta). The type species, *Tydemania expeditionis* Weber-  
41 van Bosse, was described from various places in Indonesia (Kabala Dua (Makassar Strait),  
42 Saleh bay (Sumbawa Island), de Brill, and near Fau Island) following the Siboga expedition, a  
43 Dutch scientific campaign dedicated to zoological and hydrographic research in Indonesia, led  
44 by Max Carl Wilhem Weber in 1899-1900 (Weber-van Bosse, 1901). The species was  
45 described as composed of a cylindrical monosiphonous creeping or ascending axis, either  
46 branched or unbranched. Siphonous side branches of the axis form either fans (flabella) or  
47 dense ball-like structures (glomureli). The siphons branch out dichotomously in alternate  
48 planes to form the glomeruli, or in a single plane to form the flabella. Gepp & Gepp (1911)  
49 described a second species, *Tydemania gardineri* A. Gepp & E. Gepp, from specimens  
50 collected by the British zoologist and oceanographer J. Stanley Gardiner in the central Indian  
51 Ocean (Chagos archipelago and Amirante Islands) during the Sealark expedition. *Tydemania*  
52 *gardineri* was distinguished by having only flabella and lacking glomeruli (Gepp & Gepp,  
53 1911). Nasr (1939) proposed a third species, *Tydemania mabahithae* Nasr, to accommodate  
54 specimens from the Red Sea. This species only has glomeruli and no flabella. Further studies,  
55 based on morphological observations, assumed that the presence of either flabella or  
56 glomureli alone may be explained by environmental conditions or life-stages, and that  
57 differences in siphon diameters were not significant (Gilmartin, 1966, Farghaly, 1980), and  
58 Meinesz (1981) proposed the merger of *T. gardineri* and *T. mabahithae* with *T. expeditionis*.  
59 This taxonomic decision was never confirmed by molecular data, but since then, all  
60 *Tydemania* records have been assigned to *T. expeditionis* (Guiry & Guiry 2018).

61 The rich collection of *Tydemania* samples housed at the herbarium of Noumea (NOU)  
62 and at Ghent University (GENT) offered an opportunity to revisit the genus. The collection

63 consists of 38 specimens, collected by the authors from 13 sites during several field  
64 expeditions in the Red Sea and the Indo-Pacific region, and are representative of the three  
65 morphologies, including specimens with either flabella or glomeruli only, and specimens with  
66 both. In addition, 42 digitalized specimens of *Tydemanina* spp from L were examined to  
67 support the study with reference collections.

68 The goal of this study was to take advantage of this large dataset, and to evaluate the  
69 morphology-based synonymization of *T. gardineri* and *T. mabahithae* to *T. expeditionis* using  
70 DNA analyses. Our approach consisted of: 1) applying species delimitation methods to  
71 chloroplast and nuclear markers to evaluate species boundaries; 2) analysing whether and how  
72 morpho-anatomical observations align with suggested species boundaries; and 3)  
73 reconstructing a multilocus phylogeny (*tufA*, *rbcL* and 18S rDNA) to assess the relationships  
74 of the different samples within the genus *Tydemanina*.

75

## 76 MATERIAL AND METHODS

### 77 Specimen sampling:

78 A total of 38 newly collected specimens of *Tydemanina* were included in this study. The  
79 samples were collected by SCUBA between 2005 and 2017 from many locations in the Indian  
80 Ocean (Madagascar, Mayotte, Banc du Geysir, Tanzania), the Pacific Ocean (Indonesia  
81 (Bunaken); Papua New Guinea (Kavieng & Madang); the Solomon Islands; Vanuatu; New  
82 Caledonia (Grande Terre and Loyalty islands); Fiji), and the Red Sea. Most specimens were  
83 photographed *in situ* prior to sampling, labeled and subsampled in both 95% ethanol and silica  
84 gel for later DNA analyses. Exceptions were specimens from the Solomon Islands, Vanuatu,  
85 and Fiji for which DNA extractions were done on herbarium material. Specimens were then  
86 pressed as herbarium vouchers and are currently housed at NOU and GENT. Herbarium  
87 abbreviations follow Thiers (2016).

88

89

90 ***Molecular analyses:***

91 DNA was extracted using a cetyltrimethylammonium bromide (CTAB; Doyle & Doyle, 1987)  
92 based method with modifications (available on request). Sequences from three markers  
93 (chloroplast: *tufA* and *rbcL*; nuclear: 18S rDNA) were obtained using primers previously  
94 published for the Udoteaceae family (Händeler et al., 2010; Kooistra, 2002; Lam and  
95 Zechman, 2006; Verbruggen et al., 2009) (Supplementary information, Table 1). PCR  
96 amplifications were conducted in a volume of 25 µl containing 12.5 µl AmpliTaq Gold 360  
97 Master Mix (Applied Biosystems), 0.75 µl dimethylsulfoxide (DMSO), 1 µl bovine serum  
98 albumin (BSA), 1 µl of each F and R primers (10 µM), 2.5 µl DNA extract, and 6.25 µl ultra-  
99 pure water. Marker-specific PCR programs follow Lagourgue et al. (2018), and Sanger  
100 sequencing was carried out by Genoscreen using 20 µl of PCR product (Lille, France).  
101 Sequences were quality-trimmed and aligned with Geneious version 7.1.9  
102 (<http://www.geneious.com>, Kearse et al., 2012) and the MUSCLE algorithm (Edgar, 2004) in  
103 Geneious, along with *Tydemanina expeditionis* sequences downloaded from Genbank and  
104 sequences for three outgroups: *Udotea flabellum* (J. Ellis & Solander) M. Howe, *Udotea dotyi*  
105 D.S. Littler & Littler and *Udotea geppiorum* Yamada. All the specimens used in this study  
106 along with Genbank and BOLD accession numbers are listed in Supplementary Information  
107 (Table 2).

108 ***Phylogenetic reconstructions:***

109 For the species delimitation analyses, gene trees were built using Maximum  
110 Likelihood (ML) in RAXML (Stamatakis, 2014). This was done through the CIPRES portal  
111 (Miller et al., 2010) using the GTR+G evolution model, the best scoring ML tree algorithm,

112 and 1,000 bootstrap iterations (Stamatakis et al., 2008). Data were partitioned by codon  
113 position for the *tufA* and *rbcL* datasets.

114 For phylogenetic reconstructions, the *tufA*, *rbcL* and 18S rDNA alignments were  
115 concatenated. PartitionFinder v.1.1.0 (Lanfear, et al., 2012) was used to identify the best  
116 partitioning scheme for the dataset under the BIC criterion as follows: by gene and codon for  
117 *tufA* (F81; HKY; GTR) and *rbcL* (JC; GTR+G; JC; F81; JC; HKY), and as one partition only  
118 for the 18S rDNA (HKY+I). A Bayesian phylogenetic tree was obtained using MrBayes  
119 v.3.2. (Ronquist and Huelsenbeck, 2003) through the CIPRES portal, starting from a random  
120 tree and with 10 million generations of MCMC. The convergence of the runs and ESS values  
121 were checked with Tracer 1.5. (Rambaut and Drummond, 2007). The consensus topology and  
122 the posterior probabilities were computed after removing the first 10% generations as burn-in.  
123 The ML tree was built using RAXML (Stamatakis, 2014) through the CIPRES portal. The  
124 analysis was run on the dataset partitioned by gene and codon, under a GTR+G+I nucleotide  
125 model, 1,000 rapid bootstrap replicates and search for best-scoring ML tree algorithm  
126 (Stamatakis et al., 2008).

### 127 ***Species delimitation:***

128 Species delimitation was assessed with the Automatic Barcode Gap Discovery method  
129 (ABGD, Puillandre et al., 2012), and the Poisson Tree Process method (PTP, Zhang et al.,  
130 2013). These two methods were chosen and combined for the complementarity of their  
131 underlying assumptions: ABGD is a distance-based method and attempts to identify a barcode  
132 gap between intra- and interspecific distances in the distribution of genetic distances between  
133 samples; PTP is a tree-based method and relies on the number of substitutions along branches  
134 to identify a shift between speciation and coalescence events.

135 ABGD was performed through the website [http://wwwabi.snv.jussieu.fr/public/abgd/  
136 \[abgdweb.html\]\(http://wwwabi.snv.jussieu.fr/public/abgd/abgdweb.html\)](http://wwwabi.snv.jussieu.fr/public/abgd/abgdweb.html) for each gene. The analysis was run under the simple distance method with

137 default values for all parameters. PTP was run through the Exelixis Lab web server  
138 (<http://sco.h-its.org/exelixis/web/software/PTP/index.html>) on ML rooted gene trees, for  
139 100,000 generations, a thinning value of 100, and a burn in of 10%.

140

#### 141 ***Morphological observations:***

142 Morpho-anatomical observations were made on herbarium material, decalcified in HCl  
143 solution (5%), using a binocular (WILD M3Z, Heerbrugg Switzerland) and a light microscope  
144 (Imager.A2, Zeiss, AXIO) equipped with a Canon EOS 100D digital camera. They followed  
145 the descriptions and observations from previous studies (Gepp & Gepp 1911, Weber-van  
146 Bosse 1901, and Meinesz 1981) and mainly focused on the external habit, the presence of  
147 glomeruli and flabella, the stalk (also called stipites by Gepp & Gepp 1911) and flabellum  
148 shape, the type of attachment of the stalks to the main axis of either flabella or glomeruli (Fig.  
149 1). Measurements of diameters were made for the main axis, and the stalk siphons for both  
150 flabella and glomeruli. Morphoanatomical observations and measurements are detailed in  
151 Supplementary Information (Table 3). We also made observations on the digitized herbarium  
152 specimens available online from L.

153

#### 154 **RESULTS:**

##### 155 ***Molecular results and species delimitation analyses***

156 Among the 38 *Tydemania* specimens available for molecular analysis, 35 were successfully  
157 sequenced and a total of 72 sequences were obtained, including 32 *tufA* sequences (841bp),  
158 25 *rbcL* sequences (1306 bp), and 15 18S rDNA sequences (1243 bp), and an additional 4  
159 *tufA*, 2 *rbcL*, and one 18S rDNA sequences from Genbank were added. No sequences could  
160 be obtained from the pressed herbarium sheets from Fiji, the Solomon Islands, and Vanuatu.



161 The ABGD and PTP species delimitation methods applied to the chloroplast and  
162 nuclear markers led to similar results with samples splitting into two groups (i.e., putative  
163 species) (see supplementary information: Figure 1, Data 1 and 2). The first group was  
164 composed of samples from the Red Sea (Egypt, Sudan), the Western Indian Ocean  
165 (Madagascar, the Maldives), Indonesia (Bunaken), the Philippines (Siquijor and Balicasag  
166 islands), Papua New Guinea (Madang), Japan (Kerama Islands, Okinawa) and New  
167 Caledonia. This group also included Genbank sequences of *Tydemania expeditionis* from  
168 Japan, Guam, Philippines, and Maldives. The second putative species included samples from  
169 Madagascar, Mayotte, Tanzania and the Banc du Geysir (EPI).

170

#### 171 ***Morpho-anatomical observations***

172 Photos of relevant morphological features are shown in Figures 2-24. The morphological  
173 traits of specimens from the first group matched the original description of the species  
174 *Tydemania expeditionis* (Weber-van Bosse 1901). We observed specimens with a creeping  
175 monosiphonous axis from which both glomeruli and flabella were arising (Fig. 2), while other  
176 specimens had glomeruli only (Fig. 3), or flabella only (Fig. 4). Nevertheless, common  
177 morpho-anatomical features are shared among all these specimens. *In situ*, thalli are from  
178 light to dark green with axes creeping over the substratum and, when present, glomeruli are  
179 successively stacked in an upright pompon-like structure (Fig. 3). When present, flabella are  
180 found below a series of glomeruli (Fig. 5), or arising alone along the main siphon. In both  
181 cases, the main siphon, ranging from 360 to 780  $\mu\text{m}$  in diameter (mean size = 518  $\mu\text{m} \pm 100$ ),  
182 becomes monoliform (i.e. with more constrictions) near the secondary structures (glomeruli or  
183 flabella) (Fig. 6). Flabella are generally large, monostromatic and composed of aligned and  
184 dichotomously divided siphons (Fig. 7). Some dichotomies are anisomorphic (Fig. 8). The  
185 constrictions above dichotomies show thickened cell walls. Both glomeruli and flabella are

186 supported by short and thick stalks, with few dichotomies (Fig. 9 and 10), which are attached  
187 in whorls to the main axis (Fig. 11 and 12). Glomeruli siphons range from 240 to 460  $\mu\text{m}$  at  
188 the bases, and 80 to 180  $\mu\text{m}$  (mean size= 110  $\mu\text{m} \pm 22$ ) at the apex. Flabella siphons range  
189 from 200 to 450  $\mu\text{m}$  at the base, and 60 to 130 (mean size= 79  $\mu\text{m} \pm 13$ ) at the margin. The  
190 main axis protrudes from the top of flabella or glomeruli, continuing the main growth axis of  
191 the plant (Fig. 13 and 14). A porous calcified sheath is present around the siphons.

192 The second group was characterized by specimens with only flabella arising from the  
193 main axis, while glomeruli were absent from all the specimens (Fig. 15 and 16). *In situ*, thalli  
194 form dense tufts or patches of numerous flabella, greenish-grey in color. The size of the main  
195 siphon ranges from 285 to 570  $\mu\text{m}$  (mean size= 426  $\mu\text{m} \pm 94$ ). The flabella are supported by  
196 long stalks, with strongly marked constrictions giving a beaded necklace-like aspect (Fig. 17,  
197 18 and 19). The stalks are highly dichotomously divided in alternating planes, leading to a  
198 dense and stacked mass of siphons at the basis of the flabella (Fig. 20, 21 and 22). Flabella  
199 can be of different sizes but generally small, monostromatic, and composed of dichotomously  
200 dividing siphons arranged in one plane (Fig. 24). Siphons show thickened cell walls at the  
201 strongly constricted areas above dichotomies as well as along the constrictions seen in the  
202 stalks (Fig. 23). The siphons of the flabella measure between 160 and 340  $\mu\text{m}$  at the base, and  
203 from 30 to 60  $\mu\text{m}$  (mean size= 44.5  $\mu\text{m} \pm 7$ ) at the apices. The calcified sheath of the siphons  
204 is porous. These observations correspond to the diagnosis of *Tydemanina gardineri* A. Gepp &  
205 E. Gepp. The digitized specimens L.3958458 housed in Leiden and collected in the Amirante  
206 Islands (Seychelles) by Coppejans et al. (2001) also matched the habit of the second group.

207 The siphon diameter data, acquired from a large collection of samples, highlighted that  
208 the main axis and the flabella siphons at the apices are thinner in *T. gardineri* than in *T.*  
209 *expeditionis*, a useful trait for diagnosis (Table 1). The general habit of the thalli is also useful  
210 for distinguishing between the two species, with the *T. gardineri* specimens lacking glomeruli

211 and having numerous flabella arising from the main axis, and *T. expeditionis* having only a  
212 few flabella if any. Therefore, specimens of the *T. gardineri* group appear like dense tufts or  
213 patches of flabella (Fig. 15 and 16). In *T. gardineri*, the main axis is usually creeping along  
214 the substrate rather than growing upright as in *T. expeditionis*. The form and the length of  
215 stalks supporting the flabella are also distinctive, being long, monoliform (beaded aspect), and  
216 highly dichotomously divided in *T. gardineri* (Fig. 17, 18 and 19), and shorter, stockier, and  
217 less divided in *T. expeditionis*. Morphological differences are summarized in Table 1.

218

### 219 ***Phylogenetic reconstruction***

220 The topologies of the phylogenetic trees were congruent between the markers (*tufA*, *rbcL*, and  
221 18S rDNA) when analyzed individually or concatenated. The topology as well as nodes  
222 support were similar for ML and Bayesian trees, although ML tree appeared somewhat better  
223 resolved towards the terminal branches. We considered nodes with bootstrap values (bs) > 90  
224 and Posterior Probability (PP) > 0.95 as highly supported. Both ML and BI trees show a  
225 well-supported dichotomy (bs: 100; PP: 1) separating the *Tydemanina* specimens into two  
226 fully-supported clades (bs: 100; PP: 1) (Fig. 25). The first clade grouped sequences of  
227 specimens from the Indo-Pacific and morphologically identified as *Tydemanina expeditionis*,  
228 along with sequences downloaded from Genbank. Within this clade, sequences for two  
229 specimens collected in New Caledonia grouped together in a fully supported subclade (bs: 99;  
230 PP: 0.98). The second clade included only samples collected from the Western Indian Ocean  
231 region and morphologically identified as *T. gardineri*. This clade was not subdivided in any  
232 meaningful way.

233

### 234 **DISCUSSION**

235 ***Molecular data and morphological observations support the resurrection of *Tydemanian****  
236 ***gardineri***

237 Both the molecular and morpho-anatomical analyses recovered two distinct groups of  
238 specimens among our *Tydemanian* dataset. We assigned one to *T. expeditionis* based on its  
239 morpho-anatomical similarities to the species' original description by Weber-van Bosse  
240 (1901), and the second was considered to be *Tydemanian gardineri* based on its morpho-  
241 anatomical correspondence with the diagnosis of Gepp & Gepp (1911), even though the  
242 species is currently recognized as a synonym of *T. expeditionis* (Guiry & Guiry 2019).

243 The origin of the synonymy is due to Meinesz (1981) who based his proposition on  
244 previous studies (Srinivasan, 1954; Gilmartin, 1966) as well as his own observations.

245 According to Meinesz (1981), the differences in siphon diameters between *T. expeditionis* and  
246 *T. gardineri* were not significant, and the author hypothesized that flabelliform thalli were  
247 juveniles of *T. expeditionis*, or restricted forms in unfavorable environmental conditions. Our  
248 study, however, does not support the conclusions of Meinesz (1981), and instead shows clear  
249 molecular and morphological evidence that *T. gardineri* is a distinct species. We also confirm  
250 the diagnostic characters (habit, aspect of stalks, and siphon diameters) described by Gepp &  
251 Gepp (1911) to discriminate both species.

252 We were unable to compare our specimens with the holotypes of *T. gardineri* or *T.*  
253 *expeditionis*, since none were designated by Gepp & Gepp (1911) or Weber-van Bosse  
254 (1901), and no lectotypes have been assigned since. Likewise, except for one specimen from  
255 the Amirante Islands, Seychelles (L.3958458, Coppejans et al. 2001), we have not been  
256 successful at finding other herbarium specimens previously identified as *T. gardineri*, either  
257 because there is no information about where they are housed, or because they have been  
258 merged with collections of *T. expeditionis*. Similarly, it was difficult to locate specimens of *T.*  
259 *expeditionis* but we have found the collection of Weber-van Bosse in L. None of these

260 specimens were designated as holotype at the time of description, but Weber-van Bosse  
261 described the species from this Indonesian collection, which leads us to consider these  
262 specimens as syntypes. We also were not able to sequence type specimens, or newly collected  
263 specimens from the syntype localities of *T. gardineri* (Chagos Archipelagos or Amirante  
264 islands) or *T. expeditionis* (various localities in Indonesia) in our study, but we have examined  
265 specimens from neighboring localities including Mayotte and northern Madagascar for *T.*  
266 *gardineri*, and localities in Indonesia for *T. expeditionis*. This, combined with the clear  
267 morpho-anatomical differences described above give us confidence to conclude that our two  
268 genetic lineages correspond to *T. expeditionis* and *T. gardineri*.

269         The reappraisal of *T. gardineri* raises the question of the status of a third species, *T.*  
270 *mabahithae* Nasr, which was described by Nasr (1939) as having glomeruli only. The species  
271 was also synonymized with *T. expeditionis* by Meinesz (1981) based on morphological  
272 analysis of several samples collected from the type locality (Red Sea) similar to those  
273 described by Nasr. Meinesz could not confirm differences between *T. mabahithae* and *T.*  
274 *expeditionis* based on siphon diameters or other morpho-anatomical characters (Meinesz  
275 1981). Our molecular analysis agrees with Meinesz (1981), as our sequences of Red Sea  
276 samples (Egypt, Sudan), all showing a strict glomeruli form, clearly fell in the *T. expeditionis*  
277 clade (Supplementary Information, Figure 1). Our results confirm that *T. mabahithae* should  
278 be considered a synonym of *T. expeditionis* as proposed by Meinesz (1981).

279

### 280 ***Geographical distribution of Tydemanina species***

281 Based on our data, the distribution of *Tydemanina gardineri* appears to be restricted to the  
282 Western Indian Ocean whereas *T. expeditionis* is found across the Indo-Pacific region and the  
283 Red Sea (Fig. 25). From our data, it is possible that the southwestern boundary of *T.*

284 *expeditionis* distribution be the northern coast of Madagascar, and that its easternmost  
285 distribution be Guam and Fiji. Northern Madagascar was the only locality where we found the  
286 two species in sympatry. Several records of *T. gardineri* are also reported for Taiwan (Shao  
287 2003-2014) and New Caledonia (Farghaly 1980) but these are doubtful because the  
288 identifications were based on the presence of flabella only, which is a character that can be  
289 found in *T. expeditionis*. Some New Caledonian specimens of our own collections (e.g.,  
290 NOU087203 and NOU087205) are similar in only having flabella, but grouped within the *T.*  
291 *expeditionis* clade based on DNA sequences. In the absence of DNA data, microscopic  
292 observations, which were not made in previous studies, would be needed to confidently assess  
293 identification based on siphon diameters, flabella shape and aspect of the stalk.

294

295 ***Taxonomical treatment:***

296 Based on our results, we resurrect *Tydemania gardineri*, and provide a taxonomical  
297 description of the genus *Tydemania* and its two species: *Tydemania expeditionis* Weber-van  
298 Bosse and *Tydemania gardineri* A. Gepp & E. Gepp. Despite intensive searches for specimens  
299 of *Tydemania* in various herbaria, no holotype was found. However, we found a large  
300 collection of *Tydemania expeditionis* specimens in L, including in the Weber-van Bosse  
301 Herbarium. Six of these specimens were collected during the Siboga expedition and very  
302 likely represent all or part of the specimens studied by Weber-van Bosse when writing the  
303 diagnoses of the genus and its type species *T. expeditionis* (L.3998896, L.3998892,  
304 L.3998897, L.3998894, L.3998895, L.3998893). We consider these specimens as syntype  
305 collections of *Tydemania expeditionis*. We expected to find the collection of Gepp & Gepp in  
306 BM, but were not able to find any relevant specimens there. We have been unable to identify  
307 any other herbarium housing their collection and assume that their syntype of *T. gardineri* is  
308 lost. Only one specimen of *T. gardineri* collected by E. Coppejans from near one of the

309 syntype localities was found in L (L.3958458, St. Joseph Atoll, Amirante Islands, Seychelles).  
310 We propose to designate this specimen as a neotype for *T. gardineri*. We further list reference  
311 DNA sequences of specimens of our own collection, collected near the type localities of both  
312 species. For each species, the list of specimens studied for DNA analysis and morphology is  
313 provided in Supplementary Information (Data 3)

314

315 ***Tydemanina*, Weber-van Bosse, 1901**

316 **Type species:** *Tydemanina expeditionis* Weber-van Bosse, 1901 Études sur les algues de  
317 l'Archipel Malaisien. (III). Annales du Jardin Botanique de Buitenzorg 17: 126-141, pls XVII-  
318 XIX

319 **Morpho-anatomical description** (adapted from the original description of Weber-van Bosse  
320 (1901) and new observations made here):

321 Calcareous thallus composed of a monosiphonous cylindrical axis, simple or ramified, bearing  
322 cylindrical branches with rhizoids below, and branches assembled in stacked glomeruli and/or  
323 arranged in flabella above. In the glomeruli structures, the siphons are repeatedly divided  
324 dichotomously in alternate planes and interwoven to form a dense pompon-like structure. In  
325 the flabella, siphons are divided dichotomously in one plane and are aligned and adhere to  
326 form a fan. The siphon diameter decreases towards the tips of both structures. Growth is  
327 horizontal, and in some cases vertical. Reproductive structures are unknown.

328

329 ***Tydemanina expeditionis* Weber-van Bosse, 1901. Études sur les algues de l'Archipel  
330 Malaisien. (III). Annales du Jardin Botanique de Buitenzorg 17: 39.**

331 **Syntypes:** L.3998896 (De Bril, Herb. Weber-van Bosse); L.3998893 (Banda rif, Herb.  
332 Weber-van Bosse); L.3998894 (Muaras rif; Herb. Weber-van Bosse); L.3998895 (Saleyer rif,  
333 Herb. Weber-van Bosse); L.3998892, L.3998897 (unknown locality, Herb. Weber-van Bosse)  
334 [digitized specimens available from L].

335

336 **Syntype localities:** Kabala dua reefs (Makassar Strait); Saleh bay (Sumbawa Island); de Bril,  
337 and near Fau Island (Weber-van Bosse, 1901).

338 **Morpho-anatomical description** (adapted from the original description of Weber-van Bosse  
339 (1901) and new observations made here):

340 Thallus calcified, glaucous green, with upright structures. Main axis cylindrical to moniliform  
341 or septate-like near structures, 360-780  $\mu\text{m}$  thick, with branches below bearing rhizoids, and  
342 branches above bearing glomeruli arranged in series and/or flabella. When both structures are  
343 present, flabella are found closer to the base than glomeruli. Glomeruli are composed of  
344 interwoven siphons divided dichotomously in alternate planes and form a sphere, or pompon-  
345 like structure. Glomeruli siphons measure 240-460  $\mu\text{m}$  at the base and 80-180  $\mu\text{m}$  at the  
346 apices. Flabella are monostromatic and composed of aligned siphons dichotomously divided  
347 in one plane, with symmetrical constrictions with thickened cell walls above dichotomies.  
348 Flabella are generally big and form loose groups of one to four. Flabella siphons taper from  
349 200-450  $\mu\text{m}$  at the base to 60-130  $\mu\text{m}$  at the apices. Both glomeruli and flabella structures are  
350 borne on short and stocky stalks, dividing a few times, and arising in whorls from the main  
351 axis. Growth is both horizontal and vertical, with main axes both creeping and ascending, and  
352 apices protruding at the top of flabella and/or glomeruli series.

353

354



355 **Distribution records:** Africa: Egypt (Marconi et al., 2011; this study), Tanzania\* (incl.  
356 Zanzibar) (Coppejans et al., 2000), Sudan (this study). Indian Ocean Islands: Amirante  
357 Islands\* (Silva et al., 1996), Andaman Islands \* (Silva et al., 1996), Chagos Archipelago \*  
358 (Silva et al., 1996), Maldives (Silva et al., 1996; this study), Nicobar Islands (Silva et al.,  
359 1996), Seychelles \* (Silva et al., 1996). South-west Asia: India (Silva et al., 1996; Sahoo et  
360 al., 2001; Gupta 2012; Rao & Gupta, 2015). Asia: China (Tseng, 1984; Liu, 2008), Japan  
361 (Okamura 1936; Segawa 1981, Yoshida et al., 1990; Yoshida 1998; Yoshida et al., 2015),  
362 South China Sea (Phang et al., 2016), Taiwan (Shao, 2003-2014). South-east Asia: Indonesia  
363 (Verheij & Prud'homme van Reine, 1993; Atmadja & Prud'homme van Reine, 2014),  
364 Philippines (Silva et al., 1987; Ang et al., 2014), Vietnam (Tien, 2007; Nguyen et al., 2013).  
365 Australia and New Zealand: Lord Howe Island (Lewis, 1987), Papua New Guinea (Coppejans  
366 et al., 2001), Queensland (Lewis, 1987; Phillips, 1997; Phillips, 2002; Bostock & Holland,  
367 2010). Pacific Islands: American Samoa (Skelton et al., 2004), Central Polynesia (Tsuda &  
368 Walsh, 2013), Federated States of Micronesia (Lobban & Tsuda, 2003; Tsuda 2006), Fiji  
369 (N'Yeurt et al., 1996; South & Skelton, 2003; Littler & Littler 2003; this study), Guam  
370 (Lobban & Tsuda, 2003; Lam & Zechman, 2006), Mariana Islands (Tsuda, 2003), Marshall  
371 Islands (Taylor, 1950), New Caledonia (Payri, 2007; this study), Republic of Palau (Ohba et  
372 al., 2007), Solomon Islands (Womersley & Bailey, 1970; this study), Vanuatu (this study).

373 **N.B.:** “\*” indicates localities which we suspect may be erroneous records resulting from  
374 misleading species identification (referring to *T. gardineri* rather than *T. expeditionis*) and  
375 should be confirmed with DNA sequencing or detailed anatomical analyses.

376

377 ***Tydemania gardineri* A. Gepp & E. Gepp, 1911.** The Codiaceae of the Siboga Expedition  
378 including a monograph of Flabellarieae and Udoteae Siboga-Expeditie Monographie LXII:  
379 67-68, 141, pl. XVIII: fig. 155

380 **Neotype:** L.3958458 from Seychelles, Amirante Islands, St. Joseph Atoll [digitized specimen  
381 available from L].

382

383 We have been unable to locate any of the specimens from the Gepp & Gepp collection and  
384 assume that their syntype collection of *T. gardineri* is lost. Following art. 9.8 of the CIN, we  
385 have selected the specimen above because it is from Amirante Islands (Seychelles), one of the  
386 syntype localities of *T. gardineri*.

387 **Syntype localities:** Chagos Archipelago and Amirante Islands (Gepp & Gepp, 1911)

388

389 **Morpho-anatomical description** (adapted from the original description of Gepp & Gepp  
390 (1911) and new observations made here):

391 Thallus calcified, laxly caespitose, greenish-gray, lacking glomeruli and composed of flabella  
392 only. Creeping moniliform main axis, 250-570  $\mu\text{m}$  in diameter, with sparse cylindrical  
393 branches bearing rhizoids below and branches with flabella above. Flabella are borne from  
394 long and moniliform stalks with a beaded necklace-like aspect, that are highly dichotomously  
395 divided and arise from the main axis singly or in pairs. Stalks are densely arranged and  
396 superimposed at the basis of the flabella. Flabella are small, numerous, monostromatic, and  
397 composed of aligned siphons dichotomously branched and tapering from 160-340  $\mu\text{m}$   
398 diameter at the base to 30- 60  $\mu\text{m}$  diameter at the apices. Constrictions above dichotomies are  
399 symmetric with a cell-wall thickening. Growth is horizontal.

400

401 **Distribution:** Western Indian Ocean: Chagos archipelago and Amirante Islands (Gepp &  
402 Gepp, 1911); northern Madagascar (this study), Mayotte (this study), Banc du Geysier (this

403 study), Tanzania (this study), Seychelles, Amirante Islands (Coppejans et al., 2001); Asia:  
404 Taiwan \* (Shao 2003-2004).

405 **N.B.:** the locality indicated with “\*” is suspected to be an erroneous record based on a  
406 misidentification of *T. expeditionis* specimens.

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411 Caledonia, 2012 : <http://dx.doi.org/10.17600/12100060> ; 2017 : N/O *Alis* PostBlanco1 ;  
412 Kavieng, 2014 : <http://dx.doi.org/10.17600/14004400> ; Madagascar, 2016 : MAD  
413 <http://dx.doi.org/10.17600/16004700> ; Fiji, 2007 : BSM-Fidji, 10.17600/7100030 ; Vanuatu,  
414 2006 : Santo, <http://dx.doi.org/10.17600/6100100>; Solomon Islands, 2004: BSM-Salomon,  
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425 **SUPPLEMENTARY INFORMATION**

426 Table 1: list of molecular markers and corresponding primers

427 Table 2: List of vouchers, Bold sample IDs and Genbank accession numbers

428 Table 3: Morphological observations

429 Figure 1: Maximum clade credibility tree obtained from a Beast analysis of the *tufA* collapsed  
430 dataset. The number of identical haplotypes is indicated between brackets. The origin of each  
431 sample is indicated by colored circles and correspond to the map on the right. Results of the  
432 ABGD and PTP species delimitation methods are shown and the presence of flabella (F) and  
433 glomeruli (G) is indicated.

434

435 Data 1: Overview of the ABGD and PTP species delimitation results for *rbcL*

436 Data 2: Overview of the species ABGD and PTP delimitation results for 18S rDNA

437 Data 3: List of specimens studied through molecular and morphological approaches for *T.*

438 *expeditionis* and *T. gardineri*

439 **AUTHORS CONTRIBUTIONS**

440 L. Lagourgue acquired and analyzed most molecular and morphological data, drafted and  
441 edited the manuscript; H. Verbruggen collected samples from the Red Sea and Tanzania,  
442 produced molecular data for these localities and contributed to writing and editing the  
443 manuscript; E. Ampou collected samples from Indonesia and contributed to editing the  
444 manuscript; C. Payri collected samples from various localities, and contributed to editing the  
445 manuscript.

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594 **TABLE**

595 Table 1: Morpho-anatomical characters and geographical distribution of *Tydemania*  
 596 *expeditionis* and *Tydemania gardineri* resulting from the present study, and values in bold  
 597 from the descriptions of Gepp & Gepp (1911). Values (average  $\pm$  standart deviation)

<b>Morpho-anatomical characters</b>	<i>Tydemania expeditionis</i>	<i>Tydemania gardineri</i>
<b>Habit</b>	Upright structures formed by a succession of glomeruli and/or flabella	Caespitose patch of flabella arising from a creeping main axis
<b>Glomeruli</b>	Predominant when present/ Lacking in strict flabella form	Always absent
<b>Flabella</b>	Sometimes absent (strict glomeruli form)	Always present
<b>Diameter of the main axis</b>	360 - 780 $\mu\text{m}$ (518 $\pm$ 100) <b>(450-500 <math>\mu\text{m}</math>)</b>	285 - 570 $\mu\text{m}$ (426 $\pm$ 94) <b>(250-400 <math>\mu\text{m}</math>)</b>
<b>Diameter of flabella siphons at apices</b>	60-130 $\mu\text{m}$ (79 $\pm$ 13) <b>(Min. 63 <math>\mu\text{m}</math>)</b>	30-60 $\mu\text{m}$ ( 44.5 $\pm$ 7) <b>(50-40 <math>\mu\text{m}</math>)</b>
<b>Flabella shape and number</b>	Flabella generally big and in small number (1 to 4), arising one by one or in pairs, and forming loose groups	Flabella generally small but numerous (several dozens), assembled in dense groups
<b>Stalk</b>	Short, stocky and fewly divided dichotomously (1-2)	Long, highly dichotomously divided, monoliform with

		strong constrictions (beaded siphons), crowded and superimposed at the basis of the flabella
<b>Stalk aspect</b>	Monoliform to septate	Monoliform
<b>Stalk attachment in main axis</b>	In whorls, arising in groups of two or four, on the same section of the main axis.	Simple, arising from the main axis
<b>Growth</b>	Horizontal and vertical growth (main axis both creeping and ascending)	Horizontal growth (creeping main axis only)
<b>Distribution</b>	Indo-Pacific and Red Sea	Western Indian Ocean only

598

599

600 **FIGURE LEGENDS**

601 Figure 1: Diagram showing the different morphological structures of *Tydemanina*: specimen  
602 with both glomeruli and flabella (left), and with flabella only (right).

603

604 Figures 2-14: *Tydemanina expeditionis*. Fig. 2: *In situ* habit of the thalli with flabella and  
605 glomeruli; Fig. 3: *In situ* habit of the thalli with glomeruli only; Fig. 4: *In situ* habit of the  
606 thalli with flabella only; Fig. 5: Succession of flabella and glomeruli arising from the main  
607 axis; Fig. 6: Monoliform main axis near glomeruli and flabella; Fig. 7: Siphons branching  
608 dichotomously; Fig. 8: Anisomorphic dichotomy; Fig. 9: Short and monoliform stalks with a  
609 few dichotomous divisions (flabella form) ; Fig. 10 : Short and monoliform stalks with few  
610 dichotomous divisions (glomeruli form); Fig. 11: Verticillate stalks at the basis of a flabella;  
611 Fig. 12: Verticillate stalks at the basis of a glomeruli; Fig. 13: Apex of the main axis  
612 protruding at the top of a flabella; Fig. 14: Apex of main axis protruding at the top of a  
613 glomeruli. Scale bars: Fig. 2: 0.8 cm; Fig. 3: 3.2 cm ; Fig. 4: 2 cm; Fig. 5: 3.5 mm; Fig. 6:  
614 600  $\mu\text{m}$ ; Fig. 7: 320  $\mu\text{m}$  ; Fig. 8: 160  $\mu\text{m}$ ; Fig. 9: 760  $\mu\text{m}$  ; Fig. 10: 820  $\mu\text{m}$ ; Fig. 11: 475  $\mu\text{m}$ ;  
615 Fig. 12: 800  $\mu\text{m}$ ; Fig. 13: 875  $\mu\text{m}$  ; Fig. 14: 500  $\mu\text{m}$ .

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617 Figures 15-24: *Tydemanina gardineri*: Fig. 15 and 16: *In situ* habit of a thalli with flabella  
618 only; Fig. 17-19: Groups of flabella supported by long, monoliform and highly dichotomously  
619 divided stalks; Fig. 20-22: Zoom on the beaded and crowded aspect of stalks at the basis of  
620 flabella; Fig. 23: Monoliform and strongly constricted stalks; Fig. 24: Basis of flabella  
621 showing the dichotomous branching. Scale bars: Fig. 15: 5.6 mm; Fig. 16: 7 mm ; Fig. 17: 11  
622 mm; Fig. 18: 5.8 mm; Fig. 19: 5.4mm; Fig. 20: 500  $\mu\text{m}$  ; Fig. 21: 625  $\mu\text{m}$ ; Fig. 22: 720  $\mu\text{m}$  ;  
623 Fig. 23: 350  $\mu\text{m}$ ; Fig. 24: 250  $\mu\text{m}$ .

624 Figure 25: From left to right: (1) Maximum likelihood tree reconstruction from the  
625 concatenated matrix (*tufA*, *rbcL* and 18S rDNA). Circles at each node represent ML bootstrap  
626 values (left) and posterior probabilities (right). Black circles indicate high support (bs> 90 and  
627 PP >95), grey circles indicate low support (bs<90 and PP <95), and white circles indicate  
628 incongruence between maximum likelihood and Bayesian trees. (2) Habit information for  
629 each specimen: presence of flabella (F) or glomeruli (G). (3) Grouping of sequences per  
630 marker according to the results of the species delimitation analyses (stripes indicate missing  
631 sequences). (4) Global geographical distribution. (5) Drawings showing the external habits  
632 observed for specimens in each of the two main clades. (6) Map showing the distribution of  
633 specimens from the two main clades