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Author/s:

Diaz-Tapia, P;Maggs, CA;West, JA;Verbruggen, H

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2 MS. PILAR DÍAZ TAPIA (Orcid ID : 0000-0003-4680-4867)

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8 Analysis of chloroplast genomes and a supermatrix inform reclassification of the  
9 Rhodomelaceae (Rhodophyta) <sup>1</sup>

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11 *Pilar Díaz-Tapia*<sup>2</sup>

12 Coastal Biology Research Group, Faculty of Sciences and Centre for Advanced  
13 Scientific Research (CICA), University of A Coruña, 15071, A Coruña. Spain

14 School of BioSciences, University of Melbourne, Melbourne, Victoria 3010, Australia

15 Faculty of Science and Technology, Bournemouth University, Talbot Campus, Poole,  
16 Dorset BH12 5BB, UK

17

18 *Christine A. Maggs*

19 Faculty of Science and Technology, Bournemouth University, Talbot Campus, Poole,  
20 Dorset BH12 5BB, UK

21

22 *John A. West*

23 School of BioSciences, University of Melbourne, Melbourne, Victoria 3010, Australia

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25 *Heroen Verbruggen*

26 School of BioSciences, University of Melbourne, Melbourne, Victoria 3010, Australia

27 <sup>2</sup>Author for correspondence: e-mail [pdiaz@udc.es](mailto:pdiaz@udc.es)

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29 Abstract

30 With over a thousand species, the Rhodomelaceae is the most species-rich family of red  
31 algae. While its genera have been assigned to 14 tribes, the high-level classification of  
32 the family has never been evaluated with a molecular phylogeny. Here, we reassess its  
33 classification by integrating genome-scale phylogenetic analysis with observations of  
34 the morphological characters of clades. In order to resolve relationships among the main  
35 lineages of the family we constructed a phylogeny with 55 chloroplast genomes (52  
36 newly determined). The majority of branches were resolved with full bootstrap support.  
37 We then added 266 *rbcL*, 125 18S rRNA gene and 143 *cox1* sequences to construct a  
38 comprehensive phylogeny containing nearly half of all known species in the family  
39 (407 species in 89 genera). These analyses suggest the same subdivision into higher-  
40 level lineages, but included many branches with moderate or poor support. The  
41 circumscription for nine of the 13 previously described tribes was supported, but the  
42 Lophothalieae, Polysiphonieae, Pterosiphonieae and Herposiphonieae required revision,  
43 and five new tribes and one resurrected tribe were segregated from them. Rhizoid  
44 anatomy is highlighted as a key diagnostic character for the morphological delineation  
45 of several lineages. This work provides the most extensive phylogenetic analysis of the  
46 Rhodomelaceae to date and successfully resolves the relationships among major clades  
47 of the family. Our data show that organellar genomes obtained through high-throughput  
48 sequencing produce well-resolved phylogenies of difficult groups, and their more  
49 general application in algal systematics will likely permit deciphering questions about  
50 classification at many taxonomic levels.

51

52 Key words: chloroplast genome, classification, phylogenomics, red algae,

53 Rhodomelaceae, Rhodophyta, tribes.

54 List of abbreviations: *cox1*, cytochrome oxidase subunit 1; e.g., *exempli gratia*; *rbcL*,  
55 ribulose 1,5-bisphosphate carboxylase/oxygenase large subunit; *vs.*, *versus*; 18S, small  
56 subunit ribosomal RNA gene.

57

## 58 INTRODUCTION

59 The Rhodomelaceae is the largest family of the red algae, with 1,054 species and 149  
60 genera recognized (Guiry and Guiry 2017). The number of species is probably  
61 underestimated as new taxa are often described when detailed studies using molecular  
62 data are performed (e.g., Sherwood et al. 2010, Machín-Sánchez et al. 2016, Savoie and  
63 Saunders 2016, Díaz-Tapia et al. 2017a). Moreover, there is a large number of  
64 synonyms and taxonomic entities of uncertain status, particularly in the most diverse  
65 genera such as *Polysiphonia* and *Laurencia* (Guiry and Guiry 2017). Most of these  
66 unknown entities correspond to species described in the 18<sup>th</sup> and 19<sup>th</sup> centuries and a  
67 proper reassessment may lead to the resurrection of some of these taxa. The enormous  
68 species count in the family is mirrored in high morphological diversity, particularly of  
69 vegetative organization. Thalli range from a wide variety of simple, filiform  
70 architectures to more complex pseudoparenchymatous structures, as well as diminutive  
71 parasites. The family is distinguished from other Ceramiales by a combination of  
72 vegetative and reproductive characters (Maggs and Hommersand 1993, Womersley  
73 2003). The most significant trait is the polysiphonous structure (axial cell surrounded by  
74 several pericentral cells) with monopodially developed axes.

75 The Rhodomelaceae nom. cons. was established by Areschoug (1847) as a grouping of  
76 10 genera of which only four are currently retained in the family. The first classification  
77 of the Rhodomelaceae into tribes was provided by Schmitz (1889) and later updated in  
78 Engler (1892) and in Schmitz and Falkenberg (1897). Subsequently, Falkenberg (1901)  
79 published a monumental monograph with a more extensive and detailed integrative  
80 study of the family. The 73 genera recognized by Falkenberg were classified into 12  
81 “Familien” (equivalent to tribes) and two unnamed groups, while five remained  
82 unplaced (Tables S1 and S2 in the Supporting Information). A major modification in  
83 Falkenberg’s classification was the resurrection of the family Dasyaceae Kützing (later  
84 supported by Rosenberg 1933) for a group that he considered a tribe (as “Familie”) of  
85 the Rhodomelaceae. Kylin (1956), in his classification of the red algal genera,

86 essentially followed Falkenberg's treatise, but also proposed five new "Gruppen"  
87 (equivalent to tribes: *Levringiella*, *Picconiella*, *Placophora*, *Streblocladia* and  
88 *Pleurostichidium*).

89 The most recent comprehensive classification of the family (Hommersand 1963)  
90 recognized 13 tribes and maintained three genera in an uncertain position (Tables S1  
91 and S2). Comparing Hommersand's (1963) treatise with Falkenberg's (1901)  
92 monograph, the circumscription of the tribes Amansieae, Rhodomeleae, Heterocladieae,  
93 Chondrieae, Laurencieae, Polyzonieae and Bostrychieae is the same. Although the  
94 Lophothalieae was recognized in both classifications, Hommersand (1963) included in  
95 it seven genera that Falkenberg had placed in other tribes or in the unnamed groups, as  
96 well as seven genera described after 1901. Likewise, the Pterosiphonieae was  
97 recognized by both authors, but two of its genera (*Aphanocladia* and *Pollexfenia*) were  
98 placed in the Polysiphonieae by Hommersand. A major difference between these  
99 monographs is that Hommersand merged the tribes Polysiphonieae and  
100 Herposiphonieae. Hommersand also maintained the separation of the tribes  
101 Pleurostichidieae and Streblocladieae proposed by Kylin (1956). In addition to the tribal  
102 classification, Hommersand (1963) proposed three subfamilies (Bostrychioideae,  
103 Rhodomeloideae and Polysiphonioideae), of which only the first two were maintained  
104 in a subsequent publication (Maggs and Hommersand 1993).

105 Later work on the Rhodomelaceae focused on particular taxa within the family and  
106 resulted in the recognition of 58 new or resurrected genera that were placed in  
107 previously established tribes or remain unplaced (Tables S1 and S2). Furthermore, the  
108 Brongniartelleae was segregated from the Lophothalieae (Parsons 1975), the tribe  
109 Neotenophyceae was described for the parasitic genus *Neotenophycus* (Kraft and Abbott  
110 2002), and the Sonderelleae was established for two genera previously assigned to the  
111 Delesseriaceae (Phillips 2001).

112 Since the introduction of molecular tools for macroalgal systematics, some taxa of the  
113 Rhodomelaceae have been studied in attempts to clarify relationships among genera  
114 within the Polysiphonieae (Choi et al. 2001, Bárbara et al. 2013, Díaz-Tapia et al.  
115 2017b), Pterosiphonieae (Savoie and Saunders 2016), Bostrychieae (Zuccarello and  
116 West 2006), Laurencieae (Nam et al. 1994, Martin-Lescanne et al. 2010, Cassano et al.  
117 2012, Metti et al. 2015, Machín-Sánchez et al. 2016, Rousseau et al. 2017), Amansieae  
118 (Phillips 2002a, b, Phillips and De Clerck 2005, Phillips 2006), Heterocladieae (Phillips

119 et al. 2000) and Pleurostichidae (Phillips 2000). Collectively, these studies have  
120 demonstrated that the traditionally employed molecular markers (18S rRNA and *rbcl*  
121 genes) are unable to fully resolve phylogenies, especially at the taxonomic levels of  
122 genera and tribes. This problem is particularly obvious in the Polysiphoniae (Díaz-  
123 Tapia et al. 2017b) and Bostrychieae (Zuccarello and West 2006). Other tribes  
124 (Chondrieae, Polyzoniae, Herposiphoniae, Lophothalieae) have been almost  
125 completely ignored in phylogenetic studies, and a molecular phylogeny of the whole  
126 family has never been attempted. Therefore, the current tribal classification of the  
127 family is still based almost entirely on morphological characters and the correlation  
128 between morphological and phylogenetic groups has not yet been tested.

129 Organellar phylogenomics is a valuable approach to resolving difficult phylogenies or  
130 deep level relationships in numerous groups of organisms (i.e., Ma et al. 2014, Lu et al.  
131 2015, Leliaert et al. 2016). In the red algae, the chloroplast genome is very large (about  
132 180 kb), with a highly conserved structure that includes the most diverse set of genes  
133 (about 200) known in the Archaeplastida (Janouškovec et al. 2013). However, red algae  
134 are still underrepresented in genome datasets, despite promising results whenever they  
135 have been applied to phylogenetic studies (Costa et al. 2016, Lee et al. 2016).

136 The objective of this work is to produce the first comprehensive molecular phylogeny of  
137 the Rhodomelaceae and use it to evaluate and update the high-level classification of the  
138 family. Our approach relied on resolving phylogenetic relationships among the major  
139 lineages of the Rhodomelaceae using phylogenomics based on 45 (42 newly sequenced)  
140 chloroplast genomes for selected representative taxa of the main clades of the family, as  
141 well as 11 chloroplast genomes of other Ceramiales (10 newly sequenced) to be used as  
142 outgroups. In order to get a better phylogenetic view on the rich species diversity of the  
143 family, we assembled a second dataset of 407 species in 89 genera based on more  
144 comprehensive sampling of the *rbcl*, 18S rRNA and *cox1* genes, and constructed a  
145 phylogeny constrained using the genome-scale tree as a backbone. In order to re-  
146 evaluate the tribal classification of the Rhodomelaceae we interpreted both phylogenies  
147 along with morphological characters relevant to the delineation of tribes.

148

149 MATERIALS AND METHODS

150 *Taxon sampling.* To identify the main lineages of the family Rhodomelaceae we  
151 constructed an *rbcL* phylogenetic tree including the ca. 500 sequences available in  
152 GenBank, as well as ca. 1,000 new sequences generated in our study according to  
153 methods described in Saunders and McDevit (2012). In generating new sequences, we  
154 sampled extensively in Australia, where the diversity of the Rhodomelaceae is  
155 particularly high, with nearly all tribes represented, but from where very little molecular  
156 data were available. Using a preliminary tree from this densely sampled dataset, we  
157 selected one to four species of each major lineage for high throughput sequencing. For  
158 the highly diverse (300 spp.) yet very poorly resolved tribe Polysiphonieae, 14 species  
159 were sequenced. This resulted in a total of 52 selected species (42 Rhodomelaceae and  
160 10 other Ceramiales as outgroup). Three previously recognized tribes  
161 (Pleurostichidiaceae, Heterocladaceae and the parasitic Neotenophyceae) were excluded as  
162 we could not collect new material for them. These are small tribes, containing one, three  
163 and one species, respectively.

164 *Data collection.* Total DNA was isolated with an adapted cetyltrimethylammonium  
165 bromide (CTAB) protocol (Doyle and Doyle 1987). In summary, samples were  
166 incubated for 1 h in CTAB buffer with proteinase K and extracted with 24:1  
167 chloroform:isoamyl alcohol. DNA was precipitated using 80% isopropanol at 4°C for 1  
168 h and eluted in 0.1 TE buffer.

169 Barcoded sequencing libraries (350 nt) of the 51 DNA extracts were prepared with the  
170 TruSeq Nano LT kit. Because the Verbruggen lab carries out organellar genome  
171 projects of both red and green algae, we pooled DNA extracts of red and green algae  
172 prior to library preparation, resulting in reduced costs, and the assembled genomes were  
173 separated using bioinformatics (e.g., Costa et al. 2016). Libraries were sequenced either  
174 on Illumina HiSeq 2000 at the Genome Center of the Cold Spring Harbor Marine  
175 Laboratory or Illumina NextSeq at Georgia Genomics Facility. Assembly and  
176 annotation of the genomes were performed as previously described (Verbruggen and  
177 Costa 2015, Marcelino et al. 2016). GenBank accession numbers for annotated genomes  
178 are provided in Table S3 in the Supporting Information.

179 *Sequence alignment and phylogenetic analyses.* We assembled a dataset consisting of  
180 the 51 newly sequenced chloroplast genomes, an incomplete genome (*Polysiphonia*  
181 *teges*) for which we recovered 79 genes and the four genomes previously published for  
182 the order Ceramiales (Salomaki et al. 2015, Verbruggen and Costa 2015, Hughey and

183 Boo 2016). All protein-coding genes were aligned at the amino acid level using  
184 MAFFT v7.245 (Kato and Standley 2013) using default settings and checked visually  
185 in Geneious 6.1.7. Nucleotide alignments were constructed based on the inferred amino  
186 acid alignments using TranslatorX (Abascal et al. 2010). Alignments were then  
187 concatenated and phylogenetic trees inferred with maximum likelihood (ML) in  
188 RAxML v8.0.26 (Stamatakis 2014) with GTR+ $\Gamma$  and CPREV+ $\Gamma$ +F models for the  
189 nucleotide and amino acid alignments, respectively, and using 100 traditional bootstrap  
190 replicates (Felsenstein 1985). Further analyses were carried out to assess the sensitivity  
191 of these analyses to model choice (LG, WAG) and partitioning of the data into codon  
192 positions.

193 While the chloroplast genome dataset serves to infer a solid backbone for the initial  
194 diversification of the family, it represents less than 5% of the species in the family. To  
195 obtain a tree with higher species diversity, we assembled a dataset containing 266 *rbcL*,  
196 125 18S rRNA gene and 143 *cox1* sequences for additional species, as well as 56 *rbcL*,  
197 54 18S rRNA gene and 51 *cox1* sequences for species included in the genome-scale  
198 phylogeny. Genbank accession numbers for these sequences are provided in Table S4 in  
199 the Supporting Information. The total number of species in this tree was 418: 407  
200 members of the Rhodomelaceae and 11 representatives of related families as an  
201 outgroup. The three genes were available for 89 species, but there was a substantial  
202 amount of missing data in this matrix (45%). A binary constrained phylogeny was  
203 constructed using the RAxML chloroplast genome phylogeny based on the nucleotide  
204 alignment (constructed as explained above) as the backbone and adding the  
205 concatenated alignment with the *rbcL*, 18S rRNA gene and *cox1* sequences. Data were  
206 analyzed using rapid bootstrapping in RAxML and a GTR + CAT model (Stamatakis  
207 2014). Data were partitioned to allow the more densely sampled genes (*rbcL*, *cox1* and  
208 18S rRNA gene) to have different model parameters than the remaining genes from the  
209 chloroplast genome data. Furthermore, *cox1* and *rbcL* genes were each divided into two  
210 partitions based on codon positions (1<sup>st</sup> + 2<sup>nd</sup>, 3<sup>rd</sup>).

211

## 212 RESULTS AND DISCUSSION

213 We determined 41 complete chloroplast genomes for the Rhodomelaceae, a partial  
214 genome for *Polysiphonia teges* (79 genes) and 10 complete genomes for other

215 Ceramiales to be used as outgroups. The genomes were identical in structure to those  
216 previously reported for the group (Salomaki et al. 2015, Verbruggen and Costa 2015),  
217 and a detailed description of the new genomes will be provided elsewhere. For the  
218 purpose of this paper, we required only the gene data to build alignments, and from our  
219 52 new genomes plus 4 downloaded from GenBank, a concatenated alignment of 56  
220 taxa and 194 genes (146,187 nucleotides) was obtained.

221 Chloroplast phylogenomics resolved the relationships among the major lineages of  
222 Rhodomelaceae with full support for the vast majority of branches (Fig. 1). The  
223 topology was robust to analysing the data as nucleotides or amino acids (Fig. 1 vs. Fig.  
224 S1 in the Supporting Information), different models of sequence evolution (WAG, LG;  
225 not shown) and partitioning strategies (genes, codon positions, both combined; not  
226 shown). The position of *Thaumatella adunca* is the only exception, as it was resolved  
227 with high support as sister to the Rhodomeleae in the nucleotide tree while its  
228 relationships within the family were unresolved in the amino acid tree (Fig. S1). These  
229 phylogenies include representative taxa for ten of the eleven tribes recognized in  
230 Falkenberg's (1901) classification, as well as for the Sonderelleae established by  
231 Phillips (2001). While a number of these tribes form well-supported clades in the  
232 genome-scale phylogenies, some split into different, unrelated lineages. For example,  
233 the genera *Digenea* and *Bryothamnion* are not closely related to other members of the  
234 Polysiphonieae where they are currently placed but form a separate, early-branching and  
235 well-supported lineage. Similarly, the genus *Thaumatella* is not grouped with the  
236 Lophothalieae but forms an early-branching lineage. We propose a new and the  
237 resurrection of an existing tribe for both of these early-branching lineages. The  
238 Polysiphonieae as traditionally defined forms a monophyletic clade with 96% bootstrap  
239 support in our tree, but it consists of two divergent lineages and we propose their  
240 recognition as tribes (Streblocladieae and Polysiphonieae). *Ophidocladus*, previously  
241 thought to be related to genera belonging to the Polysiphonieae, is resolved as an  
242 isolated taxon that should also be placed in its own tribe. *Herposiphonia* and  
243 *Dipterosiphonia*, two lineages currently in the Herposiphonieae, are grouped together in  
244 the trees but with poor support in the nucleotide phylogeny (66%; Fig. 1), and we  
245 propose to place them in separate tribes. The delineation of these four new tribes and the  
246 Alsidieae is further discussed below. The proposals to divide the family into three  
247 subfamilies (Bostrychioideae, for the tribe Bostrychieae; Rhodomeloideae, for the tribes

248 Rhodomeleae, Lophothalieae, Heterocladieae and Polyzonieae; and Polysiphonioideae,  
249 for the tribes Amansieae, Chondrieae, Laurencieae, Lophosiphonieae nom. nud.,  
250 Pleurostichidieae, Polysiphonieae, Pterosiphonieae and Streblocladieae nom. nud.;  
251 Hommersand 1963) or two subfamilies (Bostrychioideae for the tribe Bostrychieae, and  
252 Rhodomeloideae for the other tribes; Maggs and Hommersand 1993) are not supported  
253 in the genome-scale phylogeny.

254 With the aim of getting a more comprehensive phylogenetic view of this species-rich  
255 family, we constructed a constrained tree using the nucleotide genome-scale tree as  
256 backbone and adding 266 *rbcL*, 125 18S rRNA gene and 143 *cox1* sequences  
257 corresponding to 407 species and 89 genera of the Rhodomelaceae (Fig. S2 in the  
258 Supporting Information). A schematic representation of the tree (Fig. 2) shows that  
259 while it is congruent with the genome-scale tree, many branches were resolved with  
260 only moderate or low bootstrap support. In this tree we recognized the same tribes from  
261 the genome-scale tree except for Bostrychieae, which was paraphyletic with respect to  
262 Heterocladieae. In addition, there was a range of additional early-branching lineages  
263 without close relatives. These include the formerly recognized tribes Pleurostichidieae  
264 and Heterocladieae, the genus *Ophidocladus*, for which we propose the tribe  
265 Ophidocladeae, *Thaumatella*, for which we propose the Thaumatelleae and *Cladurus*,  
266 for which we propose the Cladureae. There were also three early-branching species  
267 (*Micropeuce strobiliferum*, *Heterodasya mucronata* and *Wilsonosiphonia howei*) whose  
268 tribal assignment requires further work. The Heterocladieae was resolved among taxa of  
269 the Bostrychieae, rendering the latter paraphyletic. However, support for this placement  
270 was very low, and it most probably resulted from missing data, because only 18S rRNA  
271 gene sequences were available for the Heterocladieae, and there were only five 18S  
272 rRNA gene sequences for the Bostrychieae (*Bostrychia simpliciuscula*, *B. tenella*, of the  
273 Peripherohapteron clade in Fig. S2; and *B. moritziana*, *Bostrychiocolax* and  
274 *Dawsoniocolax* of the Cladohapteron clade in Fig. S2).

275 Below we discuss in more detail the classification that emerged from our phylogenies.  
276 We will present the groups in the order they appear in Figure 2, from the bottom  
277 upwards. Each tribe is morphologically defined by a combination of vegetative and  
278 reproductive characters and for detailed descriptions for previously established tribes we  
279 refer to Falkenberg (1901), Hommersand (1963), Womersley (2003) and for the  
280 Sonderelleae to Phillips (2001). The brief descriptions provided below for each tribe are

281 intended to highlight easily recognizable characters, as well as propose new key  
282 characters needed to delineate some tribes. A summary of the key morphological  
283 characters delineating tribes is presented in Table S5 in the Supporting Information.  
284 More detailed descriptions of the new tribes are provided in the “Formal taxonomy”  
285 section at the end of the paper.

286 The Sonderelleae is an endemic Australasian tribe that includes two monospecific  
287 genera (*Sonderella* and *Lembergia*). Thalli consist of linear blades with a dorsiventral  
288 structure formed by three or four pericentral cells, the two laterals producing the  
289 ecorticate blade, and one or two pseudopericentrals. They lack trichoblasts; procarps  
290 and spermatangia are formed on the blade surface; and there are two tetrasporangia per  
291 segment in stichidia. Before placement in their own tribe by Phillips (2001) based on an  
292 18S rRNA gene phylogeny, *Sonderella* and *Lembergia* had been thought to be related  
293 respectively to the tribe Amansieae (Harvey 1859, Lindauer 1949, Womersley 1965,  
294 2003) and the family Delesseriaceae (Schmitz 1889, Saenger et al. 1971). Both species  
295 of the Sonderelleae were represented in the taxon-rich tree and the tribe was resolved as  
296 monophyletic with high support (Figs. 2 and S2). The genome-scale tree included  
297 *Sonderella*, and evidenced its sister relationship with the tribe Polyzonieae. Phillips  
298 (2001) had already predicted this because these are the only two tribes of the family in  
299 which three pericentral cells can be observed in certain vegetative structures of some  
300 species.

301 The Polyzonieae includes 17 species in five genera (*Cliftonaea*, *Dasyclonium*,  
302 *Echinosporangium*, *Leveillea* and *Polyzonia*) with an Indo-Pacific distribution,  
303 characterized by an elaborate structure. Thalli are strongly dorsiventral and consist of  
304 indeterminate ecorticate or corticate axes with 6 or 7 pericentral cells, bearing  
305 determinate laterals in a regular pattern. The determinate laterals have 3 pericentral cells  
306 and are simple, branched or foliose. Trichoblasts are persistent and pigmented  
307 (*Cliftonaea* and *Echinothamnion*), deciduous and unpigmented (*Leveillea*) or absent  
308 (*Dasyclonium* and *Polyzonia*). Spermatangial structures arise on determinate laterals  
309 with a sterile marginal flank, procarps and cystocarps are formed on branches or on the  
310 basal cell of a trichoblast, and the tetrasporangia are in stichidia. The genome-scale tree  
311 resolved *Cliftonaea pectinata* and *Dasyclonium flaccidum* in a strongly supported clade  
312 (Fig. 1). Likewise, our taxon-rich tree including representatives of four genera resolved  
313 the Polyzonieae as monophyletic, although with low support (Figs. 2 and S2). Our

314 results are in line with the general agreement regarding the generic composition of the  
315 tribe (Falkenberg 1901, Scagel 1953, Hommersand 1963). Interestingly, our data  
316 revealed significant cryptic diversity in *Dasyclonium incisum* (three species from  
317 Australia and one from South Africa – *rbcL* sequence divergence > 2.7 %), as well as in  
318 *Leveillea jungermannioides* (two species from Australia differing from a Korean  
319 specimen – sequence divergence > 2.1 %; the type locality is in the Red Sea).

320 The Heterocladieae is an Australian tribe with three species in the single genus  
321 *Heterocladia*, the delineation of which has been widely accepted in all previous  
322 classifications (Falkenberg 1901, Hommersand 1963, Phillips et al. 2000). It is  
323 distinguished from other Rhodomelaceae by having four pericentral cells that divide  
324 longitudinally forming 7-8 cells around the axial cell, with cortical and rhizoidal cells  
325 giving rise to a pseudoparenchymatous thallus that bears pigmented trichoblasts. The  
326 procarps and spermatangial branches are formed on trichoblasts and one  
327 tetrasporangium per segment develops in stichidia. Our taxon-rich tree included 18S  
328 rRNA gene sequences for the three known species and, in agreement with Phillips et al.  
329 (2000), the tribe was resolved as monophyletic (Figs. 2 and S2). However, it was placed  
330 together with members of the Bostrychieae in an unsupported clade, which is probably  
331 an artifact resulting from missing data. Therefore, the relationship of this tribe to other  
332 members of the family should be considered unresolved.

333 All earlier classifications recognized the Bostrychieae for the genus *Bostrychia*, as it is  
334 clearly distinguished morphologically from other Rhodomelaceae (Falkenberg 1901,  
335 Hommersand 1963). It is distributed worldwide, often in brackish environments, and is  
336 mainly characterized by its filiform habit, consisting of axes with pericentral cells  
337 dividing transversely to form tiers, the basal cell of which remains pit-connected with  
338 the axial cell. *Bostrychia* lacks trichoblasts, but has monosiphonous branches. The  
339 spermatangia and procarps are formed on determinate branches, with a particular  
340 development of female structures, and tetrasporangia form in whorls in stichidia.  
341 Furthermore, the two parasitic genera *Dawsoniocolax* and *Bostrychiocolax* were  
342 included in the tribe based on their phylogenetic affinities (Zuccarello et al. 2004). The  
343 three *Bostrychia* species for which we obtained the complete chloroplast genome were  
344 resolved in a strongly supported clade (Fig. 1). In the taxon-rich tree (Figs. 2 and S2) all  
345 *Bostrychia* species were placed together in an unsupported clade, which in turn contains  
346 two major clades, a species without close relatives and the Heterocladieae. The first

347 clade, which was poorly supported, was composed of 17 species of *Bostrychia*  
348 (Peripherohapteron-clade in Fig. S2), but the second one received high support, and  
349 contained eight *Bostrychia* species and the two monospecific parasitic genera  
350 *Dawsoniocolax* and *Bostrychiocolax* (Cladohapteron-clade in Fig. S2). These clades  
351 were named from and are in agreement with the two major groups delineated in the  
352 Bostrychieae based on the anatomy of attachment organs: peripherohapteron and  
353 cladohapteron (Zuccarello and West 2006). As discussed above, and considering the  
354 clear morphological differences, the positioning of the Heterocladieae among the  
355 Bostrychieae is very likely to be an artifact explained by the lack of overlapping markers  
356 from the two tribes in our dataset.

357 The tribe Lophothalieae included ten genera in Falkenberg's (1901) classification.  
358 Subsequently, Hommersand (1963) added another 14, seven that had been placed in  
359 different tribes by Falkenberg and seven described since 1901. Later, five newly  
360 described genera were allocated to this tribe (Joly and Oliveira Filho 1966, Wynne and  
361 Norris 1982, Noble and Kraft 1983, Millar 2000a, Huisman 2001). More recently, the  
362 two *Brongniartella* species were transferred to *Vertebrata* in the Polysiphonieae (here  
363 Streblocladieae), based on phylogenetic studies (Díaz-Tapia et al. 2017b). Therefore,  
364 the Lophothalieae currently encompasses 28 genera, each containing only one to seven  
365 species. The tribe is distributed worldwide and mainly characterized by thalli consisting  
366 of terete and radially branched axes that bear pigmented and persistent trichoblasts.  
367 Genera are delineated by characters such as the presence and degree of cortication,  
368 number of pericentral cells, trichoblast anatomy, number of sterile groups in procarps,  
369 tetrasporangial arrangement, and number and origin of cover cells (pre- or post-  
370 sporangial; Parsons 1975, Millar 2000a, Womersley 2003). On the other hand, nine  
371 genera are parasites and Hommersand (1963) placed them in this tribe mainly because  
372 they form tetrasporangia in stichidia. Our taxon-rich tree (Fig. S2) resolved with  
373 moderate support a clade including *Lophothalia hormocladus*, as well as species of  
374 *Doxodasya*, *Lophocladia*, *Murrayella*, *Spirocladia* and *Wrightiella*. This clade is  
375 represented in our genome-scale tree by *Lophocladia kuetzingii* and its phylogenetic  
376 relationships within the family are still unclear (Fig. 1). Furthermore, *Heterodasya*  
377 *mucronata* and *Micropeuce strobiliferum* are two rogue taxa in the taxon-rich tree  
378 placed as sisters to the Alsidieae and the Ophidocladieae with low support (Figs. 2 and  
379 S2). More gene sequences are needed to resolve the phylogenetic relationships of these

380 two taxa and clarify whether they are in the Lophothalieae or if they should be placed in  
381 different tribes.

382 Our phylogenies showed that the tribe Lophothalieae is not monophyletic as currently  
383 circumscribed. In addition to the above-mentioned clade and these two rogue taxa,  
384 *Thaumatella (Veleroa) adunca* was placed as sister to the Rhodomeleae with strong  
385 support in the genome-scale tree (Fig. 1). These results, together with the placement of  
386 *Brongniartella* in *Vertebrata* (as *V. byssoides* and *V. australis* in Fig. S2; Díaz-Tapia et  
387 al. 2017b), demonstrate that pigmented and persistent trichoblasts have evolved  
388 independently in several lineages of the family and further morphological traits are  
389 needed to redefine the tribe. Two schemes for subdividing the Lophothalieae have been  
390 proposed, though not generally accepted. Parsons (1975) segregated the  
391 Brongniartelleae from the Lophothalieae based on the number of sterile groups in the  
392 procarps (2/1), the absence/presence of post-sporangial tetrasporangial cover cells, and  
393 trichoblasts branched in a single plane/spirally branched/unbranched. However,  
394 Womersley and Parsons (2003) merged them again into a single tribe, suggesting that a  
395 tribal character may be the formation of tetrasporangia in stichidia without trichoblasts  
396 (*Lophocladia*, *Haplodasya*) vs. tetrasporangia on normal branches. This second  
397 proposal is not supported in our phylogeny, as *Lophocladia* is closely related to  
398 *Spirocladia barodensis* which has tetrasporangial stichidia bearing trichoblasts.  
399 Interestingly, and despite the fact that the Brongniartelleae is not supported in our  
400 phylogeny as a monophyletic taxon, four genera (*Brongniartella*, *Micropeuce*, *Veleroa*  
401 and *Heterodasya*, among the five currently recognized) that Parsons attributed to this  
402 tribe, and are represented in our taxon-rich tree, were not placed in the Lophothalieae  
403 clade. Therefore, the morphological delineation proposed by Parsons (1975) for the  
404 Lophothalieae is consistent with our phylogenies. However, some of the key  
405 reproductive characters are poorly known in several species or genera, our analysis only  
406 included representatives of nine of 19 non-parasitic genera currently assigned to the  
407 tribe, and the phylogenetic relationships of *Micropeuce* and *Heterodasya* are  
408 unresolved. Therefore, it is not yet possible to provide an accurate delineation for the  
409 Lophothalieae and further morphological and molecular studies are needed to clarify the  
410 systematics of this group. The systematics of *Thaumatella (Veleroa) adunca*, a  
411 morphologically distinctive species with respect to other Lophothalieae, is discussed  
412 below.

413 The circumscription of the Amansieae is identical in Falkenberg (1901) and  
414 Hommersand (1963), who both assigned nine genera to this tribe. Four new genera have  
415 subsequently been included in the Amansieae (Wilson and Kraft 2000, Phillips 2002b,  
416 2006). The tribe includes about 60 species, and is particularly diverse on Australian and  
417 South African shores. It is characterized by pseudoparenchymatous thalli, mostly  
418 complanate or leaf-like, with strong dorsiventrality involving trichoblasts arising  
419 adaxially at the apices and, in most species, the differentiation of pericentral cells into  
420 lateral, dorsal and ventral positions. The procarps and spermatangial branches are  
421 formed on modified trichoblasts and the tetrasporangia, two per segment, usually form  
422 in stichidia. Our genome-scale and taxon-rich trees (Figs. 1, 2 and S2), including  
423 representatives of two and 13 genera, respectively, resolved the Amansieae as  
424 monophyletic with strong support. Although relationships among species within the  
425 tribe in the taxon-rich tree are in general not well supported, our data suggest that a  
426 revision is needed at generic level, as *Amansia*, *Vidalia* and *Osmundaria* are apparently  
427 not monophyletic.

428 The monospecific genus *Cladurus*, endemic to Australia, was included in the tribe  
429 Chondrieae in earlier classifications (Falkenberg 1901, Hommersand 1963). However,  
430 Gordon-Mills and Womersley (1987) and Womersley (2003) considered that it did not  
431 belong to this tribe because spermatangial branches are cylindrical instead of plate-like,  
432 as is characteristic in the Chondrieae. Furthermore, this genus is distinguished from  
433 other Rhodomelaceae by its terete thalli with five pericentral cells,  
434 pseudoparenchymatous construction with light cortication so that the segments are  
435 conspicuous in surface view in branches, cystocarps arising on short axillary branches  
436 and tetrasporangia borne in stichidia. This species was only included in the taxon-rich  
437 tree, where it was placed as sister to the Alsidieae, but with low support. Considering  
438 the peculiar morphological characters of this genus and its ambiguous relationships with  
439 other members of the family, we propose the Cladureae trib. nov.

440 The small genera *Alsidium*, *Bryothamnion* and *Digenea* (8, 3 and 2 species respectively)  
441 were previously included in the Polysiphonieae (Falkenberg 1901, Hommersand 1963).  
442 The genome-scale tree (Fig. 1) placed *Bryothamnion* and *Digenea* in a single clade with  
443 strong support, sister to the clade formed by the Chondrieae and Laurencieae. The  
444 taxon-rich phylogeny (Fig. S2) resolved *Alsidium*, *Bryothamnion* and *Digenea* in a  
445 moderately supported clade. These three genera have pseudoparenchymatous thalli with

446 5-12 pericentral cells, forming axes of indeterminate growth usually clothed with short  
447 determinate branches. Furthermore, they differ from the Polysiphonieae by having  
448 plate-like spermatangial branches without sterile margins (Falkenberg 1901, Børgesen  
449 1920, Norris 1994). These spermatangial branches resemble the typical ones of the  
450 Chondrieae, however, in the Chondrieae they have marginal sterile cells and all species  
451 have 5 pericentral cells. Therefore, based on the morphology and the phylogeny we  
452 propose the resurrection of the tribe Alsidieae for these three genera (discussed in the  
453 formal taxonomic treatment below). According to the taxon-rich tree, two main clades  
454 are resolved in the tribe and *Alsidium* is not monophyletic. Considering that *A.*  
455 *corallinum* from the Mediterranean is the type of the genus, *A. cymatophilum* from  
456 Hawaii must be transferred to *Digenea*. Furthermore, the separation between  
457 *Bryothamnion* and *Alsidium* requires further investigation.

458 Generic composition of the Chondrieae was very similar in Falkenberg's (1901) and  
459 Hommersand's (1963) classifications. Falkenberg included six genera, one later  
460 transferred to the Lophothalieae by Hommersand (1963), who also added two newly  
461 described genera. Subsequently, *Waldoia* and the parasitic genera *Ululania*, *Benzaitenia*  
462 and *Jantinella* were included in this tribe (Taylor 1962, Morrill 1976, Apt and Schleich  
463 1998, Kurihara et al. 2010). The genome-scale phylogeny (Fig. 1) includes three  
464 *Chondria* species that constitute a monophyletic clade. Similarly, the taxon-rich  
465 phylogeny (Fig. S2) includes representatives from nine of the 11 genera currently  
466 assigned to the tribe which, except for *Cladurus* (see above), are resolved in a  
467 monophyletic clade with moderate support. Our data also suggest that the tribe requires  
468 a revision at the genus level because neither *Chondria*, currently including 80 species,  
469 nor *Acanthophora* (7 species), is monophyletic.

470 The tribe Laurencieae was likewise very similar in generic composition in Falkenberg's  
471 (1901) and Hommersand's (1963) classifications, encompassing the large genus  
472 *Laurencia* (145 currently recognized species), *Rodriguezella* and the parasitic  
473 *Janczewskia*. Subsequently, six other genera were reinstated or segregated for groups of  
474 species previously assigned to *Laurencia* (Nam et al. 1994, Nam 2007, Martin-  
475 Lescanne et al. 2010, Cassano et al. 2012, Metti et al. 2015, Rousseau et al. 2017). The  
476 genome-scale and taxon-rich phylogenies (Figs. 1 and S2), with representatives of seven  
477 genera, resolved all members of the tribe as a single clade that respectively received  
478 high or moderate support.

479 A close relationship between the Chondrieae and Laurencieae was previously predicted  
480 in evolutionary reconstructions of the family based on morphological characters  
481 (Falkenberg 1901, Hommersand 1963) and is strongly supported in our phylogenies  
482 (Figs. 1 and 2). Both tribes are distributed worldwide and characterized by  
483 pseudoparenchymatous thalli, such that the segments and pericentral cells are not  
484 distinguishable in surface view. They differ in the number of pericentral cells (5 in the  
485 Chondrieae and 2 or 4 in the Laurencieae) and the anatomy of the male structures  
486 (plate-like spermatangial branches with sterile marginal cells in the Chondrieae and  
487 modified trichoblasts or filaments immersed in apical depressions in the Laurencieae).

488 *Ophidocladus simpliciusculus* was included in Falkenberg's (1901) classification in the  
489 "Lophosiphonia group" (Lophosiphonieae nom. nud. in Hommersand 1963), a group of  
490 genera with dorsiventral prostrate and erect ecorticate terete axes and exclusive  
491 production of endogenous branches. Although this group resembles various tribes in  
492 some of its characters, it could not be assigned to any of them (Falkenberg 1901).

493 *Ophidocladus simpliciusculus* is separated out in our genome-scale and taxon-rich  
494 phylogenies (Figs. 1 and 2) and it has numerous characters that make it unique within  
495 the family, such as a large axial cell surrounded by up to 28 pericentral cells, alternately  
496 arranged trichoblasts and spermatangial structures covering the two basal dichotomies  
497 of a trichoblast (Saenger 1971, Díaz-Tapia and Bárbara 2013). On the basis of its  
498 morphology and our molecular evidence we propose Ophidocladeae trib. nov. for this  
499 monospecific genus.

500 The genus *Veleroa* is currently placed in the tribe Lophothalieae (Dawson 1944,  
501 Hommersand 1963); *V. adunca* is the only one of the seven species in this genus  
502 included in our analysis (as *Thaumatella adunca*; see below). It was placed as a taxon  
503 without close relatives, sister to the Rhodomeleae, with high and moderate support in  
504 the genome-scale and taxon-rich trees (Figs. 1 and 2), respectively. The type species of  
505 *Veleroa* is *V. subulata* from California and the genus is characterized by ecorticate axes  
506 with four pericentral cells, pigmented unbranched trichoblasts and one tetrasporangium  
507 per segment on branches bearing trichoblasts (Dawson 1944). *Veleroa adunca*, by  
508 contrast, has branched trichoblasts (Womersley and Parsons 2003). Furthermore, the  
509 detailed description of *V. subulata* (Abbott and Ballantine 2012) based on topotype  
510 material reveals additional important differences between them. *Veleroa adunca* has  
511 rhizoids cut off from a single pericentral cell as multicellular, but uniseriate, filaments

512 that terminate in a multicellular discoid pad (Fig. 2H); rhizoids in *V. subulata* have  
513 multiseriate rhizoidal filaments formed from two adjoining pericentral cells (Abbott and  
514 Ballantine 2012; Fig. 2N). Also, the spermatangial organs differ in these species – they  
515 are ovoid, with a single basal sterile cell in *V. adunca*, while they are cylindrical with  
516 long basal and apical sterile filaments in *V. subulata*. When Womersley and Parsons  
517 (2003) transferred *Dasya adunca* to *Veleroa* they also placed *Thaumatella disticha*, the  
518 type of the genus, in synonymy. They argued that the characters used by Kylin (1956) to  
519 separate *Thaumatella* from *Veleroa*, i.e., branching patterns, were misinterpreted.  
520 However, differences in the anatomy of rhizoids and spermatangial organs suggest that  
521 *V. adunca* and *V. subulata* most probably belong to different genera. Therefore, we  
522 propose to resurrect the genus *Thaumatella* for *Veleroa adunca*. Furthermore,  
523 considering the position of this species in the phylogeny and its unique rhizoid anatomy  
524 (differing from other *Veleroa* – see also *V. mangeana* [Millar 2000b, Schneider et al.  
525 2010] – and members of the Lophothalieae, when information is available), we propose  
526 the Thaumatelleae trib. nov.

527 The Rhodomeleae includes *Rhodomela* and *Odonthalia*, both placed in this tribe by  
528 Falkenberg (1901) and Hommersand (1963), as well as the subsequently described  
529 *Neorhodomela* (Masuda 1982) and *Beringiella* (Wynne 1980). Their distribution is  
530 restricted to cold shores of the Northern Hemisphere. They are characterized by having  
531 pseudoparenchymatous thalli, with 6-7 pericentral cells dividing transversely and the  
532 apical cell retaining the pit connection with the axial cell. The taxon-rich tree (Fig. 2),  
533 including representatives of three genera, resolves the tribe in a highly supported clade.  
534 Furthermore, three parasites (*Harveyella*, *Leachiella* and *Choreocolax*), whose  
535 placement in the Rhodomelaceae was clarified in Zuccarello et al. (2004), were also  
536 resolved in this tribe in our phylogeny. The tribe is represented in the genome-scale tree  
537 (Fig. 1) by *R. confervoides* and *C. polysiphoniae* and was placed as sister to  
538 *Thaumatella* and in turn to the Polysiphonieae.

539 The Pterosiphonieae was erected by Falkenberg (1901) for six genera that share a  
540 bilateral branching pattern, with the branches congenitally fused to the main axes to a  
541 varying extent, ranging from filiform to foliose thalli. They have procarps and  
542 spermatangia on modified trichoblasts and tetrasporangia on lateral branches.  
543 Hommersand (1963) pointed out that *Tayloriella*, *Rhodomelopsis* and *Carradoria* (as  
544 *Carradoriella*) of the Polysiphonieae, all erected after 1901, must be in this tribe

545 although they lack congenital fusion of branches. Consequently, he redefined the tribe  
546 mainly by the alternate-distichous branching pattern and the absence of vegetative  
547 trichoblasts, and he transferred *Aphanocladia* and *Pollexfenia* to the Polysiphonieae.  
548 Only two genera have subsequently been placed in this tribe, *Xiphosiphonia*, recently  
549 segregated from *Pterosiphonia*, and *Heterostroma* (Kraft and Wynne 1992, Savoie and  
550 Saunders 2016).

551 The taxon-rich tree (Fig. S2), including 10 representatives of the 12 genera assigned to  
552 the tribe at one time, resolved a moderately supported clade comprising *Pterosiphonia*  
553 and seven other genera previously assigned to the Pterosiphonieae. However,  
554 *Pterochondria* and *Carradoria* (as *P. virgata*) were placed in the Polysiphonieae (here  
555 clade Streblocladieae) despite having the characters of the tribe Pterosiphonieae.  
556 Furthermore, the clade Pterosiphonieae included five additional genera, *Lophurella*,  
557 *Echinothamnion* and *Periphykon*, currently included in the Polysiphonieae, *Gredgaria*  
558 of the Herposiphonieae and *Womersleyella* currently lacking tribal assignment. Also, an  
559 unidentified species of Pterosiphonieae was resolved in this clade with high support,  
560 and three other *Polysiphonia*-like species were placed as sister to this clade with low  
561 support (their taxonomic identity at generic and species level requires further work).

562 This tribe is represented in the genome-scale tree (Fig. 1) by members of four genera  
563 (*Symphyocladia*, *Dictyomenia*, *Periphykon* and *Gredgaria*) that form a strongly  
564 supported clade, which in turn is sister with moderate support to the clade formed by  
565 two "*Polysiphonia*" spp. Among the genera placed for the first time in the  
566 Pterosiphonieae, *Gredgaria* is the only one that meets Falkenberg's or Hommersand's  
567 criteria for delineating the tribe, despite being included by Womersley (2003) in the  
568 Herposiphonieae. By contrast, the other genera or species have trichoblasts, and/or  
569 branches spirally arranged and not congenitally fused with the main axes (Hollenberg  
570 1967, Womersley 2003, P. Díaz-Tapia, pers. obs.). Therefore, the morphological criteria  
571 used for distinguishing the Pterosiphoniae from the Polysiphonieae are not supported.

572 While all genera with an alternate branching pattern and congenitally fused branches are  
573 in the Pterosiphonieae (except *Pterochondria*), the tribe also includes several members  
574 with spirally arranged branches not congenitally fused with the main axes. Also the  
575 presence/absence of trichoblasts varies among members of the tribe. However, a  
576 character that we found uniformly in all the species placed in this tribe in our phylogeny  
577 is that rhizoids are cut off from the distal (and proximal in *Gredgaria* and

578 Pterosiphonieae sp.) ends of the pericentral cells, and the rhizoidal filament terminates  
579 in several cells forming a multicellular discoid pad (Fig. 2, E-G). This character is  
580 distinctive with respect to the Polysiphonieae and Streblocladieae, in which the rhizoids  
581 are unicellular and are formed from the mid-proximal ends of the pericentral cells.

582 *Lampisiphonia* is the only known exception among the species placed in the  
583 Streblocladieae in our phylogeny, as it has multicellular rhizoids (some rhizoids of the  
584 thallus have multicellular filaments, and discoid pads are multicellular when mature).  
585 However, they are formed from the proximal ends of the pericentral cells (Fig. 2B;  
586 Bárbara et al. 2013, P. Díaz-Tapia, pers. obs.).

587 The Herposiphonieae is found worldwide and is characterized by a dorsiventral and  
588 filiform habit, thalli consisting of ecorticate axes with 4-16 pericentral cells and the  
589 exclusive production of endogenous branches with defined sequences of determinate  
590 and indeterminate branches. Procarps and spermatangia are formed on modified  
591 trichoblasts and tetrasporangia on determinate branches. The tribe was erected by  
592 Falkenberg (1901) for seven genera, but Hommersand (1963) merged it with the  
593 Polysiphonieae, distinguishing the genera of this tribe as “dorsiventral Polysiphonieae”.  
594 *Streblocladia* and the parasite *Microcolax* were moved to a separate “Gruppe” by Kylin  
595 (1956), which was recognized as the tribe Streblocladieae nom. nud. by Hommersand  
596 (1963), as discussed below. On the other hand, four genera described since 1963  
597 (*Herposiphoniella*, *Ditria*, *Gredgaria* and *Tiparria*) have been attributed to the  
598 Herposiphonieae (Hollenberg 1967, Womersley 2003). In summary, nine genera are  
599 currently assigned to the tribe Herposiphonieae, of which *Herposiphonia* contains 56  
600 species, *Dipterosiphonia* seven and the other genera only one to three species. They are  
601 distinguished by distinct branching patterns. Three of them were included in our  
602 analysis, but *Gredgaria* was transferred to the Pterosiphonieae (see above). The other  
603 two, *Herposiphonia* and *Dipterosiphonia*, were placed together in a poorly supported  
604 clade, sister to the Pterosiphonieae in the genome-scale tree (Fig. 1). The taxon-rich tree  
605 placed them, with *Wilsonosiphonia* and *Pleurostichidium*, in a poorly supported clade  
606 (Fig. 2).

607 *Pleurostichidium* is a morphologically very distinctive monospecific genus placed in its  
608 own tribe, the Pleurostichidiaceae, for which Phillips (2000) provided a detailed  
609 characterization. Considering that the Dipterosiphonieae and Herposiphonieae clades  
610 are strongly supported, the early divergence of these two lineages as well as the

611 Pleurostichidae, and the extent to which *Pleurostichidium* differs morphologically  
612 from the Herposiphoniae, we propose the segregation of the tribe Dipterosiphoniae  
613 from the Herposiphoniae. The tribal assignment of *Wilsonosiphonia* requires a better  
614 understanding of its phylogenetic relationships and further studies using more gene data  
615 are needed. The Dipterosiphoniae and Herposiphoniae differ from the Polysiphoniae  
616 and share with the Pterosiphoniae rhizoids cut off from the distal end of pericentral  
617 cells. All have multicellular discoid pads, which have the same structure in the  
618 Dipterosiphoniae and Pterosiphoniae. By contrast, in the Herposiphoniae, discoid  
619 pads consist of a digitate structure formed by an extension of the rhizoidal filament that  
620 divides to form small apical cells (Fig. 2D). Furthermore, the Herposiphoniae is  
621 characterized by its distinctive regular pattern of the formation of determinate and  
622 indeterminate branches, often in a 3:1 sequence. The tribe Dipterosiphoniae, by  
623 contrast, is distinguished by producing alternate pairs of determinate branches.  
624 However, as only seven species are currently known, it remains to be determined  
625 whether this branching pattern applies more generally.

626 The Polysiphoniae is the largest tribe of the Rhodomelaceae and has a worldwide  
627 distribution. Falkenberg (1901) included 11 genera characterized by filiform thalli,  
628 heavily corticated in a few species, with branches radially organized and trichoblasts  
629 deciduous and unpigmented. Subsequently, another 11 newly described or resurrected  
630 genera, three of them parasitic, were included in this tribe. While some genera in this  
631 tribe (*Echinothamnion*, *Lophurella*, *Digenea*, *Alsidium*, *Bryothamnion*) are here  
632 transferred to other tribes (see discussion on Alsidiae and Pterosiphoniae), the vast  
633 majority are placed in a monophyletic clade that was resolved with high and moderate  
634 support in the genome-scale and taxon-rich phylogenies, respectively (Figs. 1, 2 and S2;  
635 Streblocladiae and Polysiphoniae clades). Two major lineages were resolved within  
636 this clade and we propose to segregate the tribe Streblocladiae from the  
637 Polysiphoniae. They are distinguished by the synapomorphic trait of having rhizoids  
638 cut off from the mid-proximal end of the pericentral cells (Streblocladiae, Fig. 2A) vs.  
639 rhizoids in open connection with the pericentral cells (Polysiphoniae; Fig. 2C; Kim and  
640 Lee 1999, Choi et al. 2001, Díaz-Tapia et al. 2017b).

641 The Polysiphoniae clade contains the type of the genus *Polysiphonia* (*P. stricta*) and it  
642 was termed *Polysiphonia* sensu stricto in previous phylogenetic studies of the tribe  
643 (Choi et al. 2001, Bárbara et al. 2013, Díaz-Tapia et al. 2017b). These studies

644 emphasized the existence of two major clades within *Polysiphonia sensu stricto* (here  
645 named *Polysiphonia* and *Bryocladia/Falkenbergiella* in Fig. S2), and they were  
646 resolved as monophyletic or paraphyletic in previous works depending on the taxon  
647 selection and the molecular marker(s) considered. *Polysiphonia* and  
648 *Bryocladia/Falkenbergiella* are represented in our genome-scale tree by *P. stricta* and  
649 *P. scopulorum* and are definitively resolved as a monophyletic clade sister to  
650 Strebocladieae (Fig. 1). In the taxon-rich tree (Fig. S2) *Polysiphonia* and  
651 *Bryocladia/Falkenbergiella* contain eight and 10 species and are resolved as two highly  
652 supported clades. The clade containing *P. stricta* corresponds to the genus *Polysiphonia*  
653 and all the species have four pericentral cells, are decumbent or erect and have  
654 predominantly exogenous branches. The other clade is morphologically more variable  
655 and includes species with a dorsiventral or radial structure, with predominantly  
656 exogenous or endogenous branches, and with four or more (*Bryocladia*) pericentral  
657 cells. The generic assignment of this second clade requires further studies including  
658 analysis of material of *Falkenbergiella capensis* from South Africa (currently included  
659 in *Lophosiphonia*), with morphological traits (four pericentral cells, dorsiventral, with  
660 endogenous branches) that indicate it may be included in this clade, and the scarcely  
661 known *Bryocladia cervicornis* from Java. These two species are the types of their  
662 corresponding genera, *Bryocladia* pre-dating *Falkenbergiella*.

663 In addition to these two previously recognized groups in *Polysiphonia sensu stricto*, *P.*  
664 *teges* was also resolved in this clade (Fig. 1). In the taxon-rich phylogeny (Fig. S2), *P.*  
665 *teges* is closely related to *Lophosiphonia simplicissima* and *L. obscura sensu* (1956,  
666 with six pericentral cells; see Rueness 1971, Silva 1996, Díaz-Tapia and Bárbara 2013,  
667 for a further discussion on the taxonomic identity of this species), the type species of  
668 *Lophosiphonia*. We propose to maintain the generic attribution of this clade to  
669 *Lophosiphonia* and transfer *P. teges* to this genus. *Lophosiphonia* was erected by  
670 Falkenberg (in Schmitz and Falkenberg 1897) to group species with a secondary  
671 dorsiventral structure and predominantly endogenous branches. However, the validity of  
672 this circumscription has been discussed (Díaz-Tapia and Bárbara 2013 and references  
673 therein) and finally rejected on the basis of molecular and morphological evidence, as  
674 species meeting these criteria have very different affinities with other members of the  
675 Polysiphonieae (e.g., *L. reptabunda* is in *Vertebrata* and *L. scopulorum* in  
676 *Bryocladia/Falkenbergiella*). The main character distinguishing *Lophosiphonia sensu*

677 stricto from the Streblocladieae is that rhizoids are in open connection with the  
678 pericentral cells (P. Díaz-Tapia & C.A. Maggs, pers. obs.). It differs from other  
679 Polysiphonieae by having more than four pericentral cells (*Bryocladia* is an exception).  
680 Furthermore, the characters proposed by Falkenberg to delineate this genus are shared  
681 by all members of the clade, and are also present in other genera. *Lophosiphonia*  
682 *prostrata* is also resolved as sister to this clade but with moderate support and it differs  
683 from other *Lophosiphonia* species because it is always epiphytic on brown algae in the  
684 Zonarieae, with the apices curled over the host, growing synchronously with it, and is  
685 completely prostrate except for the branches bearing reproductive structures  
686 (Womersley 2003, P. Díaz-Tapia, pers. obs.). We propose *Epizonaria* gen. nov. for this  
687 species. Our phylogenies reveal that Falkenberg's "Lophosiphonia group" (equivalent  
688 to Hommersand's tribe Lophosiphonieae nom. nud.) is not phylogenetically supported,  
689 as the type species of the genus *Lophosiphonia* is placed with high support in the  
690 Polysiphonieae. Among the genera included in the *Lophosiphonia* group by Falkenberg,  
691 *Ctenosiphonia* has been merged with *Vertebrata* (Díaz-Tapia et al. 2017b) and  
692 *Pleurostichidium* and *Ophidocladus* represent separate tribes (Hommersand 1963, this  
693 study). Finally, in addition to the three clades discussed above, three small unidentified  
694 *Polysiphonia*-like species collected on Australian coral reefs and at Rottnest Island  
695 (Western Australia) were resolved as sisters to the *Bryocladia/Falkenbergiella* clade  
696 with low support. They are very similar in morphology to other small Polysiphonieae,  
697 as they have four pericentral cells and unicellular rhizoids in open connection to  
698 pericentral cells. They may constitute new genera, but further studies are required.

699 The Streblocladieae clade includes eight genera, as well as a number of clades and taxa  
700 for which generic assignment needs further investigation. The parasite *Aiolocolax*  
701 *pulchellus* was placed in this clade but with low support. Previously this species was  
702 considered incertae sedis, even at family level (Pocock 1956). Here, we propose the  
703 tribe Streblocladieae for this clade. This name was used before by Kylin (1956, as  
704 *Streblocladia* "Gruppe") and by Hommersand (1963, Streblocladieae nom. nud.) but, as  
705 discussed above, we propose a different circumscription, defined by unicellular rhizoids  
706 cut off from the mid-proximal ends of pericentral cells. Kylin's and Hommersand's  
707 concept was of a tribe containing species similar to *Polysiphonia* but with primary  
708 dorsiventrality, which is not supported in our phylogeny. The genus *Streblocladia*,

709 including the type species *S. glomerulata*, is placed among radially branched species in  
710 phylogenetic analyses (Díaz-Tapia et al. 2017b; Fig. S2).

711

## 712 CONCLUSIONS

713 The phylogenies presented here are based on the most comprehensive molecular dataset  
714 analyzed to date for the family Rhodomelaceae, both in terms of number of genes (198  
715 for the genome-scale phylogeny) and number of taxa (407 for the taxon-rich  
716 phylogeny). The relationships among the major clades of the family received very  
717 strong support in the genome-scale phylogeny including 44 species from 16 tribes (11  
718 previously established and five proposed here), demonstrating the strength of  
719 chloroplast genome data to resolve challenging phylogenies in the red algae.

720 Conversely, the taxon-rich phylogeny resolved the majority of branches with moderate  
721 to low support, suggesting that the chloroplast genomes of many more species are  
722 required to fully understand the phylogeny of the family. An integrative analysis of the  
723 two phylogenies and the morphological characters of the identified lineages have led us  
724 to thoroughly evaluate previous classification schemes and propose the first subdivision  
725 of the family Rhodomelaceae into tribes supported by molecular data.

726 The genome-scale and taxon-rich molecular phylogenies of the family Rhodomelaceae  
727 supported recognition of the 12 tribes previously proposed in Falkenberg's (1901) and  
728 Hommersand's (1963) classifications, as well as the tribe Sonderelleae (Phillips 2001).  
729 By contrast, the Lophosiphonieae and the division of the family into subfamilies  
730 proposed by Hommersand (1963) and Maggs and Hommersand (1993) were not  
731 supported. Our analysis, representing 89 genera of the Rhodomelaceae, corroborates the  
732 previously established circumscriptions of the tribes Sonderelleae, Polyzonieae,  
733 Heterocladieae, Bostrychieae, Amansieae, Rhodomeleae, Chondrieae (except *Cladurus*,  
734 as predicted by Womersley 2003), Laurencieae and Pleurostichidieae. A very different  
735 scenario emerged for the tribes Lophothalieae, Pterosiphonieae, Herposiphonieae and  
736 Polysiphonieae. Not surprisingly, these four tribes include most of the members of the  
737 family with terete ecorticate or slightly corticate filiform thalli (apart from the  
738 Bostrychieae and some Polyzonieae), the simplest morphological architecture in the  
739 Rhodomelaceae.

740 A tribe is resurrected (Alsidieae) and three new tribes are here proposed  
741 (Dipterosiphonieae, Thaumatelleae and Streblocladieae) to accommodate genera  
742 previously placed in the Lophothalieae, Herposiphonieae, Polysiphonieae and  
743 Pterosiphonieae. Furthermore, several genera are transferred from the Polysiphonieae  
744 (and Streblocladieae) to the Pterosiphonieae and vice versa. Therefore, the  
745 morphological delineation of these tribes requires reassessment and we propose rhizoid  
746 anatomy as a key diagnostic character. Free rhizoids are the attachment structures of  
747 most Rhodomelaceae, while basal discs have evolved in the largest species. Although  
748 rhizoids are small structures, they are morphologically very variable, as previously  
749 described (e.g., Hollenberg 1967, Womersley 2003, Zuccarello and West 2006,  
750 Bustamante et al. 2017; Fig. 2). However, their relevance in delineating tribes was not  
751 previously highlighted (see McIvor 2000). Rhizoid anatomy is particularly useful in  
752 delineating the tribes Streblocladieae, Polysiphonieae, Herposiphonieae and  
753 Pterosiphonieae/Dipterosiphonieae (Table S5; Fig. 2), as some of their species are very  
754 similar in other morphological characters. Furthermore, the Thaumatelleae, Polyzonieae  
755 and Bostrychieae also have distinctive rhizoids (Fig. 2), although there are many other  
756 key characters for delineating them at the tribal level.

757 The resurrected tribe Alsidieae is recognized as independent from the Polysiphonieae  
758 and is characterized by having corticate and radially branched indeterminate axes and  
759 plate-like spermatangial branches. The delineation of the tribe Lophothalieae is more  
760 problematic, as it is not monophyletic as originally conceived (*Brongniartella* was  
761 merged with *Vertebrata* and *Thaumattella* was segregated as a separate tribe).  
762 Furthermore, the relationships of *Micropeuce* and *Haplodasya* within the family are still  
763 unclear and further investigations, including more extensive taxon and gene sampling,  
764 are needed to clarify their tribal placement and determine the actual circumscription of  
765 the tribe Lophothalieae. Finally, the genus *Ophidocladus*, previously included in the  
766 Lophosiphonieae nom. nud., was also allocated to its own tribe. In addition to the tribal  
767 level results emerging from this work, our phylogenies showed that an integrative  
768 review at the genus level is especially needed in the tribes Chondrieae, Amansieae and  
769 Streblocladieae.

770 The family Rhodomelaceae includes 48 species of parasites in 26 genera separated from  
771 non-parasitic species. However, the few previous investigations on parasites involving  
772 molecular data and our phylogenies (including ten species and 9 genera) have all

773 demonstrated that they are often closely related to non-parasitic species and their  
774 separation as independent genera is not always supported (Zuccarello et al. 2004,  
775 Kurihara et al. 2010, Preuss et al. 2017). The available molecular data suggest that  
776 species of *Janczewska*, *Benzaitenia*, *Ululania*, *Dawsoniocolax* and *Bostrychiocolax*  
777 belong to genera with non-parasitic type species. We do not make nomenclatural  
778 proposals here, pending revisions of these genera. By contrast, our data support the  
779 recognition of *Leachiella*, *Harveyella*, *Choreocolax* and *Aiolocolax* as separate genera,  
780 but their phylogenetic relationships within the tribes are still not well resolved. These  
781 four genera previously lacked tribal attributions and our phylogenies revealed that the  
782 first three are in the Rhodomeleae, while *Aiolocolax* is in the Streblocladiaceae. In  
783 addition to the above-mentioned taxa, five parasitic genera are unclassified at a tribal  
784 level, one was placed in an independent tribe and 11 were included in five other tribes.  
785 Assigning parasitic genera to tribes based on morphological characters is not supported.  
786 For example, nine parasitic genera were included in the Lophothalieae mainly because  
787 they have tetrasporangia in whorls (Hommersand 1963), but several parasites with  
788 sporangia in whorls do not belong in the Lophothalieae (e.g., *Aiolocolax*, *Ululania*). The  
789 morphological characters of parasites, with very reduced vegetative structures, are  
790 markedly different from the non-parasitic members of their corresponding tribes and are  
791 always exceptions to the morphological delineations established for the tribes.

792 Besides the tribal classification of the Rhodomelaceae, Falkenberg (1901, p. 700) and  
793 Hommersand (1963, p. 343) reconstructed the phylogenetic relationships among tribes  
794 based on morphology. While use of the wide variety of morphological characters is  
795 reliable for delineating tribes, reconstructing their phylogenetic relationships on this  
796 basis it is much more difficult. Interpretations provided by Falkenberg (1901) and  
797 Hommersand (1963) agreed in recognizing the Bostrychieae on the basis of the  
798 phylogeny and considering the Laurencieae and the Chondrieae as closely related tribes,  
799 which were all supported in our molecular phylogeny (Fig. 1). Otherwise, their  
800 interpretations differed greatly and also are very different from our results (Fig. 1). For  
801 example, the Polyzonieae was considered related to the Rhodomeleae by Hommersand  
802 (1963), Falkenberg (1901) allied this tribe to the Herposiphonieae and our phylogeny  
803 resolved it as sister to the Sonderelleae and the Bostrychieae (Fig. 1). Differences  
804 between morphological and molecular phylogenies may result from the fact that  
805 characters classically used for establishing tribal relationships (e.g., dorsiventrality,

806 pigmented trichoblasts, reproductive structures on specialized branches) evolved  
807 independently several times in the history of the family.

808 In addition to the 407 species and 89 genera represented in our phylogeny, there are  
809 currently 647 species and 60 genera in the family Rhodomelaceae for which molecular  
810 data are not available at present. Further investigations are needed to unravel their  
811 phylogenetic relationships and reassess their classification. Among them, some taxa,  
812 such as *Pachychaeta*, *Rhodolachne*, *Stichothamnion*, *Oligocladus*, and  
813 “*Lophosiphonia*” *mexicana*, have very unusual morphological characteristics (Weber-  
814 van Bosse 1911, Dawson 1944, Hommersand 1963, Vroman 1967, Womersley and  
815 Bailey 1970, Wynne 1970). This paper provides the first global phylogenetic study of  
816 the family Rhodomelaceae, but much work remains, especially at lower taxonomic  
817 levels, to fully understand the systematics of the most diverse family of the red algae.

818

#### 819 FORMAL TAXONOMY

##### 820 *Taxonomic proposals at tribe level*

821 Cladureae Díaz-Tapia & Maggs, trib. nov.

822 Diagnosis: Thalli erect, attached by a holdfast, radially branched, with a protruding  
823 apical cell surrounded by deciduous trichoblasts. Axes terete, with 5 (-6) pericentral  
824 cells, 1-3 layers of cortical cells developing close to the apices, but the segments  
825 remaining obvious throughout branches in surface view. Rhizoids cut off from  
826 pericentral cells, surrounding the axial and pericentral cells in older parts of the thallus.  
827 Spermatangial branches cylindrical, arising on branches of trichoblasts; cystocarps  
828 formed on axillary branchlets; one tetrasporangium per segment, cut off from the  
829 pericentral cells, formed in stichidia arising in axils of lateral branches.

830 *Type and only genus: Cladurus* Falkenberg in Schmitz and Falkenberg 1897: 435.

831

832

833 Dipterosiphonieae Díaz-Tapia & Maggs, trib. nov.

834 Diagnosis: Thalli entirely or largely prostrate, formed by axes of indeterminate growth  
835 bearing branches of determinate growth in alternate pairs. Rhizoids cut off from the  
836 distal ends of pericentral cells of prostrate axes, terminating in multicellular haptera.  
837 Axes with 4-10 pericentral cells, ecorticate. All branches exogenous. Trichoblasts, when  
838 present, only on determinate branches, deciduous. Spermatangial branches cylindrical,  
839 formed on modified trichoblasts; one tetrasporangium per segment in determinate  
840 branches. Cystocarps ovoid.

841 *Type and only genus: Dipterosiphonia* F.Schmitz & Falkenberg 1897: 463.

842

843 Ophidocladeae Díaz-Tapia & Maggs, trib. nov.

844 Diagnosis: Thalli dorsiventral, consisting of an extensive prostrate system bearing  
845 rhizoids ventrally and erect axes dorsally. Rhizoids cut off from the middle or proximal  
846 ends of pericentral cells, terminating in multicellular discoid pads. Axes ecorticate; erect  
847 axes composed of a large axial cell and 16-28 pericentrals. All branches endogenous.  
848 Trichoblasts deciduous, alternately arranged. Spermatangial structures formed on  
849 branched trichoblasts, each covering the two basal dichotomies, with a quadrifurcate  
850 appearance; procarps formed on trichoblasts, with two sterile groups, cystocarps ovoid;  
851 two tetrasporangia per segment in lateral branches with two cover cells.

852 *Type and only genus: Ophidocladus* Falkenberg in Schmitz and Falkenberg 1897: 461.

853

854

855 Streblocladieae Díaz-Tapia & Maggs, trib. nov.

856 Hommersand's (1963) proposal of the Streblocladieae was invalid because it lacked a  
857 formal description. Considering that we are proposing a very different concept for the  
858 tribe than that established by Hommersand (1963) and formerly by Kylin (1956, as  
859 *Streblocladia* "Gruppe"), here we propose a new tribe.

860 Diagnosis: Thalli predominantly erect, decumbent or dorsiventral (erect and prostrate  
861 axes). Axes with 4-24 pericentral cells, ecorticate or corticate. Rhizoids cut off from  
862 mid-proximal ends of pericentral cells, normally unicellular (multicellular in  
863 *Lampisiphonia*), occasionally absent in largest species and in the obligate epiphyte

864 *Vertebrata lanosa*. Trichoblasts deciduous and unpigmented when mature (except *V.*  
865 *byssoides* and *V. australis*). Spermatangial branches cylindrical, borne on modified  
866 trichoblasts or on one or two branches of trichoblasts; procarps formed on modified  
867 trichoblasts, with 2 sterile groups; one tetrasporangium per segment (two in  
868 *Leptosiphonia* and *Ctenosiphonia*) on main axes or lateral branches.

869 Type genus: *Streblacladia* F.Schmitz in Schmitz and Falkenberg 1897: 457-458.

870 Other genera of this tribe included in our molecular analysis: *Aiolocolax* M.A.Pocock,  
871 1956: 22, *Lampisiphonia* H.G.Choi, Díaz-Tapia & Bárbara in Bárbara et al. 2013: 138,  
872 *Leptosiphonia* Kylin 1956: 509, *Melanothamnus* Bornet & Falkenberg in Falkenberg  
873 1901: 684, *Pterochondria* Hollenberg 1942: 532-533, *Polyostea* Ruprecht 1850: 231,  
874 *Tolypiocladia* F.Schmitz in Schmitz and Falkenberg 1897: 441-442, *Vertebrata*  
875 S.F.Gray 1821: 338.

876

877 Thaumatelleae Díaz-Tapia & Maggs, trib. nov.

878 Diagnosis: Thalli predominantly prostrate, radially branched, with 4 ecorticate  
879 pericentral cells. Rhizoids cut off from pericentral cells, with a uniseriate multicellular  
880 filament terminating in multicellular haptera. Trichoblasts pigmented and persistent,  
881 branched 1-3 times. Spermatangial branches formed on trichoblasts, often several per  
882 trichoblast, ovoid, lacking basal and sterile apical cells; cystocarps strongly urceolate;  
883 one tetrasporangium per segment on lateral branches bearing trichoblasts.

884 Type and only genus: *Thaumatella* (Falkenberg) Kylin 1956: 511.

885

886 Amended descriptions of tribes

887 Alsidieae Ardissonne 1883: 352.

888 Diagnosis: Thalli erect, attached by a holdfast or a basal crust, consisting of axes of  
889 indeterminate growth, radially branched, and clothed in some species with branches of  
890 determinate growth. Trichoblasts, if present, deciduous. Axes terete or complanate, with  
891 5-12 pericentral cells, corticated from close to the apices with 1-2 layers of cortical  
892 cells. Spermatangial branches plate-like, lacking sterile marginal cells; one  
893 tetrasporangium per segment. Cystocarps globose.

894 *Type: Alsidium* C.Agardh 1827: 639.

895 *Other genera of this tribe included in our molecular analysis: Digenea* C.Agardh 1822:  
896 388-389, *Bryothamnion* Kützing 1843: 433.

897 Nomenclatural note: although J.Agardh (1863) provided a diagnosis for the tribe  
898 Alsidaeae, he included this “tribus” and other tribes as sections of the Ordo Rhodomeleae  
899 so it is not valid under ICBN Art. 37.6-8 which states that names of taxa with misplaced  
900 rank are invalid. Therefore the first valid publication of the tribe Alsidaeae was by  
901 Ardissonne (1883).

902

903 *Herposiphoniaeae* F.Schmitz & Falkenberg 1897: 457.

904 Description: Thalli formed by axes of indeterminate growth, prostrate or partially erect,  
905 which bear axes of determinate growth that are simple and erect. Rhizoids cut off from  
906 the distal ends of pericentral cells of prostrate axes, terminating in multicellular haptera  
907 that consist of the extension of the rhizoidal filament into a digitate structure that  
908 divides to form small terminal cells. Axes with 6-16 pericentral cells, ecorticate. All  
909 branches exogenous, formed on consecutive segments in a pattern that consists of one  
910 branch of indeterminate growth followed by three determinate branches. Some species  
911 have naked segments and more determinate branches separate indeterminate axes.  
912 Trichoblasts only on determinate branches, deciduous and unpigmented when mature.  
913 Spermatangial branches cylindrical, formed on modified trichoblasts; cystocarps  
914 terminal or subterminal on determinate branches; one tetrasporangium per segment on  
915 determinate branches.

916 Genus of this tribe included in our molecular analysis: *Herposiphonia* Nägeli 1846: 238.

917

918 *Polysiphoniaeae* F.Schmitz 1889: 447.

919 Description: Thalli predominantly erect, decumbent or dorsiventral (erect and prostrate  
920 axes). Axes with 4 (-7-11) pericentral cells, ecorticate. Rhizoids in open connection  
921 with pericentral cells, unicellular. Trichoblasts, when present, deciduous and  
922 unpigmented at maturity. Spermatangial branches cylindrical, formed on modified  
923 trichoblasts or on one or two branches of trichoblasts; prococarps formed on modified

924 trichoblasts, with two sterile groups; one tetrasporangium per segment on main axes or  
925 lateral branches with two or three cover cells. Cystocarps globose or ovoid.

926 Genera of this tribe included in our molecular analysis: *Bryocladia* F.Schmitz in  
927 Schmitz and Falkenberg 1897: 442, *Epizonaria* Díaz-Tapia & Maggs gen. nov.,  
928 *Lophosiphonia* Falkenberg in Schmitz and Falkenberg 1897: 459-460, *Polysiphonia*  
929 Greville 1823: 210.

930

931

932 Pterosiphonieae Falkenberg 1901: 261.

933 Description: Thalli ranging from largely prostrate to erect, bilaterally or radially  
934 branched, usually with erect axes of determinate growth bearing determinate laterals  
935 that remain completely free, or are congenitally fused with the main axes to different  
936 degrees, forming foliose thalli in genera with branches fused along the whole length  
937 with the main axes. Attachment by holdfasts in the largest species or by rhizoids cut off  
938 from the distal ends of pericentral cells of prostrate axes (in some genera also from  
939 proximal ends in adjoining pericentral cells), terminating in multicellular haptera  
940 formed by cell divisions at the end of the rhizoidal filament. Axes with 4-14 pericentral  
941 cells, ecorticate to heavily corticate. Trichoblasts varying from rare and formed only on  
942 reproductive branches, to common in determinate branches, deciduous. Spermatangial  
943 branches cylindrical, formed on modified trichoblasts; one tetrasporangium per segment  
944 on determinate branches, with two pre-sporangial and one post-sporangial cover cells.

945 Genera of this tribe included in our molecular analysis: *Amplisiphonia* Hollenberg 1939:  
946 380, *Aphanocladia* Falkenberg in Schmitz and Falkenberg 1897: 444, *Dictyomenia*  
947 Greville 1830: 1, *Echinothamnion* Kylin 1956: 506, *Gredgaria* Womersley 2003: 314-  
948 315, *Lophurella* Schmitz in Schmitz and Falkenberg 1897: 440-441, *Periphykon*  
949 Weber-van Bosse 1929: 255, *Pollexfenia* Harvey 1844: 431, *Pterosiphonia* Falkenberg  
950 in Schmitz and Falkenberg 1897: 443, *Rhodomelopsis* M.A.Pocock 1953: 34,  
951 *Symphyclocladia* Falkenberg in Schmitz and Falkenberg 1897: 443-444, *Womersleyella*  
952 Hollenberg 1967: 213, *Xiphosiphonia* Savoie & Saunders 2016: 933.

953

954 Taxonomic proposals at genus level

955 *Epizonaria* Díaz-Tapia & Maggs, gen. nov.

956 Diagnosis: Vegetative thalli entirely prostrate, attached by unicellular rhizoids in open  
957 connection with the pericentral cells. Axes with four pericentral cells, ecorticate.  
958 Reproductive structures on short erect axes. Trichoblasts, if present, on erect branches,  
959 deciduous. Spermatangial branches on modified trichoblasts; cystocarps terminal on  
960 erect branches, ovoid to slightly urceolate; one tetrasporangium per segment.

961 Type species: *Epizonaria prostrata* (Harvey) Díaz-Tapia & Maggs, comb. nov.

962 Basionym: *Polysiphonia prostrata* Harvey, 1855. Some account of the marine botany of  
963 the colony of western Australia. *Trans. R. I. Acad.* 22:525–66.

964 Synonyms: *Lophosiphonia prostrata* (Harvey) Falkenberg; *Falkenbergiella prostrata*  
965 (Harvey) Kylin.

966 Etymology: From the Greek prefix epi (on) and the genus name *Zonaria*, as the type  
967 species of the genus is epiphytic on members of the Zonarieae.

968

969 Amended descriptions of genera

970 *Lophosiphonia* Falkenberg in Schmitz and Falkenberg 1897: 459-460.

971 Description: Thalli consisting of prostrate and erect axes, endogenously branched. Axes  
972 ecorticate, with 6-7 pericentral cells. Rhizoids in open connection with pericentral cells,  
973 unicellular. Trichoblasts deciduous when present. Spermatangial branches cylindrical,  
974 formed on modified trichoblasts; cystocarps ovoid; one tetrasporangium per segment.

975 Type species: *Lophosiphonia obscura* (C.Agardh) Falkenberg in Schmitz and  
976 Falkenberg 1897: 460.

977 Species of this genus included in our molecular analysis: *L. simplicissima* Díaz-Tapia in  
978 Díaz-Tapia and Bárbara 2013: 356, *Lophosiphonia teges* (Womersley) Díaz-Tapia &  
979 Maggs, comb. nov.

980

981 Taxonomic proposals at species level

982 *Digenea cymatophila* (R.E.Norris) Díaz-Tapia & Maggs, comb. nov.

983 Basionym: *Alsidium cymatophilum* R.E.Norris 1994, p. 434: Some cumophytic  
984 Rhodomelaceae (Rhodophyta) occurring in Hawaiian surf. *Phycologia* 33:434–43.  
985  
986 *Lophosiphonia teges* (Womersley) Díaz-Tapia & Maggs, comb. nov.  
987 Basionym: *Polysiphonia teges* Womersley 1979: 494, Southern Australian species of  
988 *Polysiphonia* Greville (Rhodophyta). *Aust. J. Bot.* 27:459–528.  
989  
990 *Thaumatella adunca* (J.Agardh) Díaz-Tapia & Maggs, comb. nov.  
991 Basionym: *Dasya adunca* J.Agardh 1890: 112-113, Till algernes systematik. Nya  
992 bidrag. (Sjette afdelningen.). *Lunds Universitets Års-Skrift, Andra Afdelningen, Kongl.*  
993 *Fysiografiska Sällskapets i Lund Handlingar* 26:1–125.  
994 Synonyms: *Brongniartella disticha* Falkenberg; *Thaumatella disticha* (Falkenberg)  
995 Kylin; *Veleroa adunca* (J.Agardh) Womersley & M.J.Parsons.

996

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1012

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1305 45.
- 1306
- 1307 Figure legends.

1308

1309 FIG. 1. Phylogeny of the family Rhodomelaceae indicating tribes with light or dark  
1310 shaded areas; the unshaded area corresponds to the outgroup. Resurrected (Alsidieae)  
1311 and new tribes are indicated with bold font. RAxML tree based on nucleotide alignment  
1312 of the 198 concatenated genes from the chloroplast genome. All branches have full  
1313 bootstrap support (\*), except those where bootstrap values are indicated on branches.

1314 FIG. 2. Compressed phylogeny of 16 clades and seven isolated taxa. The width of each  
1315 triangle is proportional to the number of species from that clade included in the analysis.  
1316 The RAxML tree used the genome-scale phylogeny based on nucleotides as a constraint  
1317 and incorporated 322 *rbcL*, 179 18S rRNA gene and 194 *cox1* sequences for a total of  
1318 418 species. Bootstrap values are indicated on branches when 100 (\*) or > 50%. Black  
1319 triangles and bold names represent resurrected (Alsidieae) and new tribes, while gray  
1320 triangles represent previously recognized tribes. The complete phylogeny is presented in  
1321 Figure S2. Schematic representations of the rhizoid anatomy and cladohapteron (panel  
1322 K) are provided indicating their corresponding tribes with capital letters, when  
1323 applicable (basal discs characterizes tribes without diagrams). Panel N corresponds to  
1324 *Veleroa subulata*, which was not included in our phylogeny and is currently placed in  
1325 the Lophothalieae.

1326 FIG. S1. Phylogeny of the family Rhodomelaceae indicating tribes with light or dark  
1327 shaded areas, the unshaded area corresponds to the outgroup. Resurrected (Alsidieae)  
1328 and new tribes are indicated with bold font. RAxML tree based on protein alignment of  
1329 the 198 concatenated genes from the chloroplast genome. All branches have full  
1330 bootstrap support (\*), except those where bootstrap values are indicated on branches.

1331 FIG. S2. Phylogeny of the family Rhodomelaceae. The RAxML tree used the genome-  
1332 scale phylogeny based on nucleotides as a constraint and incorporated 322 *rbcL*, 179  
1333 18S rRNA gene and 194 *cox1* sequences for a total of 418 species. Bootstrap values are  
1334 indicated on branches 100 (\*) or > 50%. Species names in bold correspond to type  
1335 species of genera. Note: *Dasyclonium incisum*, *Leveillea jungermannioides*,  
1336 *Dipterosiphonia dendritica* and *Herposiphonia tenella* are the type species of their  
1337 corresponding genera, but considering the cryptic diversity found in these species, we  
1338 are unable to determine at present which of them, if any, should be considered as the  
1339 type.

- 1340 Table S1. Alphabetical list of genera currently recognized in the Rhodomelaceae  
1341 indicating their tribal placement in Falkenberg's (1901) and Hommersand's (1963)  
1342 classifications and the tribal assignment of genera described after 1963, as well as the  
1343 positions resulting from this work.
- 1344 Table S2. Generic composition of the rhodomelacean tribes in Falkenberg's (1901) and  
1345 Hommersand's (1963) classifications. The tribal placement of genera described after  
1346 1963 is also indicated, as well as the generic composition of tribes resulting from this  
1347 work. N.d. = no data; d.p. = different position.
- 1348 Table S3. GenBank accession numbers of the chloroplast genomes included in the  
1349 phylogenetic analysis.
- 1350 Table S4. GenBank accession numbers of the sequences included in the phylogenetic  
1351 analysis. Numbers printed in bold correspond to newly determined sequences.
- 1352 Table S5. Key morphological characters delineating the tribes of the Rhodomelaceae.



