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Analysis of chloroplast genomes and a supermatrix inform reclassification of the Rhodomelaceae (Rhodophyta) [1]

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Abstract

With over a thousand species, the Rhodomelaceae is the most species-rich family of red algae. While its genera have been assigned to 14 tribes, the high-level classification of the family has never been evaluated with a molecular phylogeny. Here, we reassess its classification by integrating genome-scale phylogenetic analysis with observations of the morphological characters of clades. In order to resolve relationships among the main lineages of the family we constructed a phylogeny with 55 chloroplast genomes (52 newly determined). The majority of branches were resolved with full bootstrap support. We then added 266 *rbc*L, 125 18S rRNA gene and 143 *cox*1 sequences to construct a comprehensive phylogeny containing nearly half of all known species in the family (407 species in 89 genera). These analyses suggest the same subdivision into higher-level lineages, but included many branches with moderate or poor support. The circumscription for nine of the 13 previously described tribes was supported, but the Lophothalieae, Polysiphonieae, Pterosiphonieae and Herposiphonieae required revision, and five new tribes and one resurrected tribe were segregated from them. Rhizoid anatomy is highlighted as a key diagnostic character for the morphological delineation of several lineages. This work provides the most extensive phylogenetic analysis of the Rhodomelaceae to date and successfully resolves the relationships among major clades of the family. Our data show that organellar genomes obtained through high-throughput sequencing produce well-resolved phylogenies of difficult groups, and their more general application in algal systematics will likely permit deciphering questions about classification at many taxonomic levels.

54 List of abbreviations: *cox*1, cytochrome oxidase subunit 1; e.g., *exempli gratia*; *rbc*L,

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 18th and 19th 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 Bostrychiae 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 Pleurostichidieae (Phillips 2000). Collectively, these studies have

120 demonstrated that the traditionally employed molecular markers (18S rRNA and *rbc*L

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 Polysiphonieae (Díaz-

123 Tapia et al. 2017b) and Bostrychieae (Zuccarello and West 2006). Other tribes

124 (Chondrieae, Polyzonieae, Herposiphonieae, 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 *rbc*L, 18S rRNA and *cox*1 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 *rbc*L 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 (Pleurostichidieae, Heterocladieae 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   MAFFTv7.245 (Katoh 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+Γ and CPREV+Γ+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 *rbc*L,

196   125 18S rRNA gene and 143 *cox*1 sequences for additional species, as well as 56 *rbc*L,

197   54 18S rRNA gene and 51 *cox*1 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 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 *rbc*L, 18S rRNA gene and *cox*1 sequences. Data were

206   analyzed using rapid bootstraping in RAxML and a GTR + CAT model (Stamatakis

207   2014). Data were partitioned to allow the more densely sampled genes (*rbc*L, *cox*1 and

208   18S rRNA gene) to have different model parameters than the remaining genes from the

209   chloroplast genome data. Furthermore, *cox*1 and *rbc*L genes were each divided into two

210   partitions based on codon positions (1st + 2nd, 3rd).

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 *rbc*L, 125 18S rRNA gene and 143 *cox*1 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 – *rbc*L 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   Bostrychiae 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 hormoclados*, 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 Ophidocladeae 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 Schlech

463   1998, Kurihara et al. 2010). The genome-scale phylogeny (Fig. 1) includes three

464   *Chondria* species that consitute 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 Pleurostichidieae, 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 Pleurostichidieae, and the extent to which *Pleurostichidium* differs morphologically

612 from the Herposiphonieae, we propose the segregation of the tribe Dipterosiphonieae

613 from the Herposiphonieae. 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 Dipterosiphonieae and Herposiphonieae differ from the Polysiphonieae

616 and share with the Pterosiphonieae rhizoids cut off from the distal end of pericentral

617 cells. All have multicellular discoid pads, which have the same structure in the

618 Dipterosiphonieae and Pterosiphonieae. By contrast, in the Herposiphonieae, 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 Herposiphonieae 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 Dipterosiphonieae, 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 Polysiphonieae 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 Alsidieae and Pterosiphonieae), 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 Streblocladieae and Polysiphonieae clades). Two major lineages were resolved within

636 this clade and we propose to segregate the tribe Streblocladieae from the

637 Polysiphonieae. They are distinguished by the synapomorphic trait of having rhizoids

638 cut off from the mid-proximal end of the pericentral cells (Streblocladieae, Fig. 2A) vs.

639 rhizoids in open connection with the pericentral cells (Polysiphonieae; Fig. 2C; Kim and

640 Lee 1999, Choi et al. 2001, Díaz-Tapia et al. 2017b).

641 The Polysiphonieae 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 Streblocladieae (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 *Thaumatella* 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 *Janczewskia*, *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 Streblocladieae. 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: *Streblocladia* 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 stongly 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 Ardissone 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   Alsideae, 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 Alsideae was by
901   Ardissone (1883).

902

903   Herposiphonieae 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   Polysiphonieae 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; procarps 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   *Symphyocladia* 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

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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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1306

1307 Figure legends.
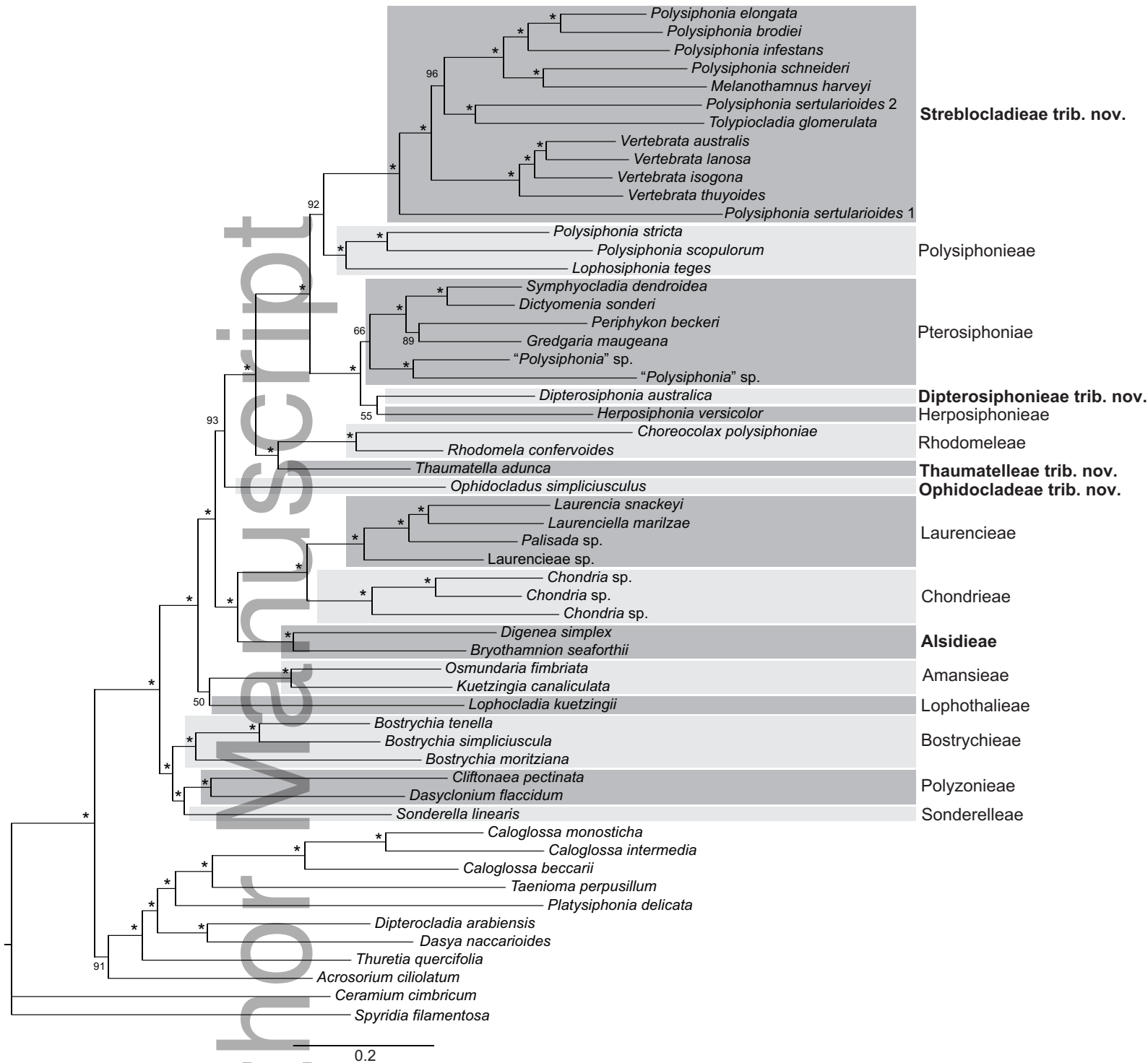
1308

1309   F<small>IG</small>. 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

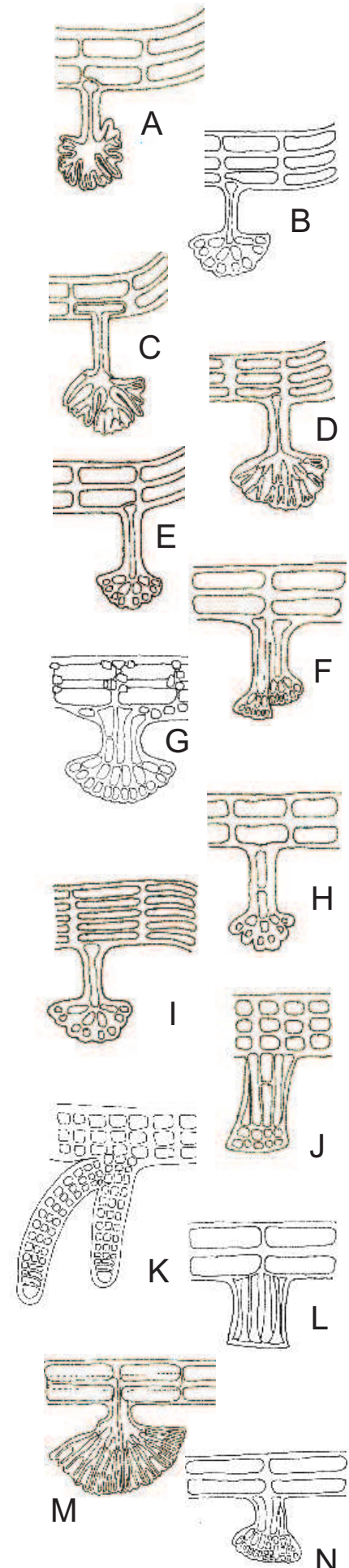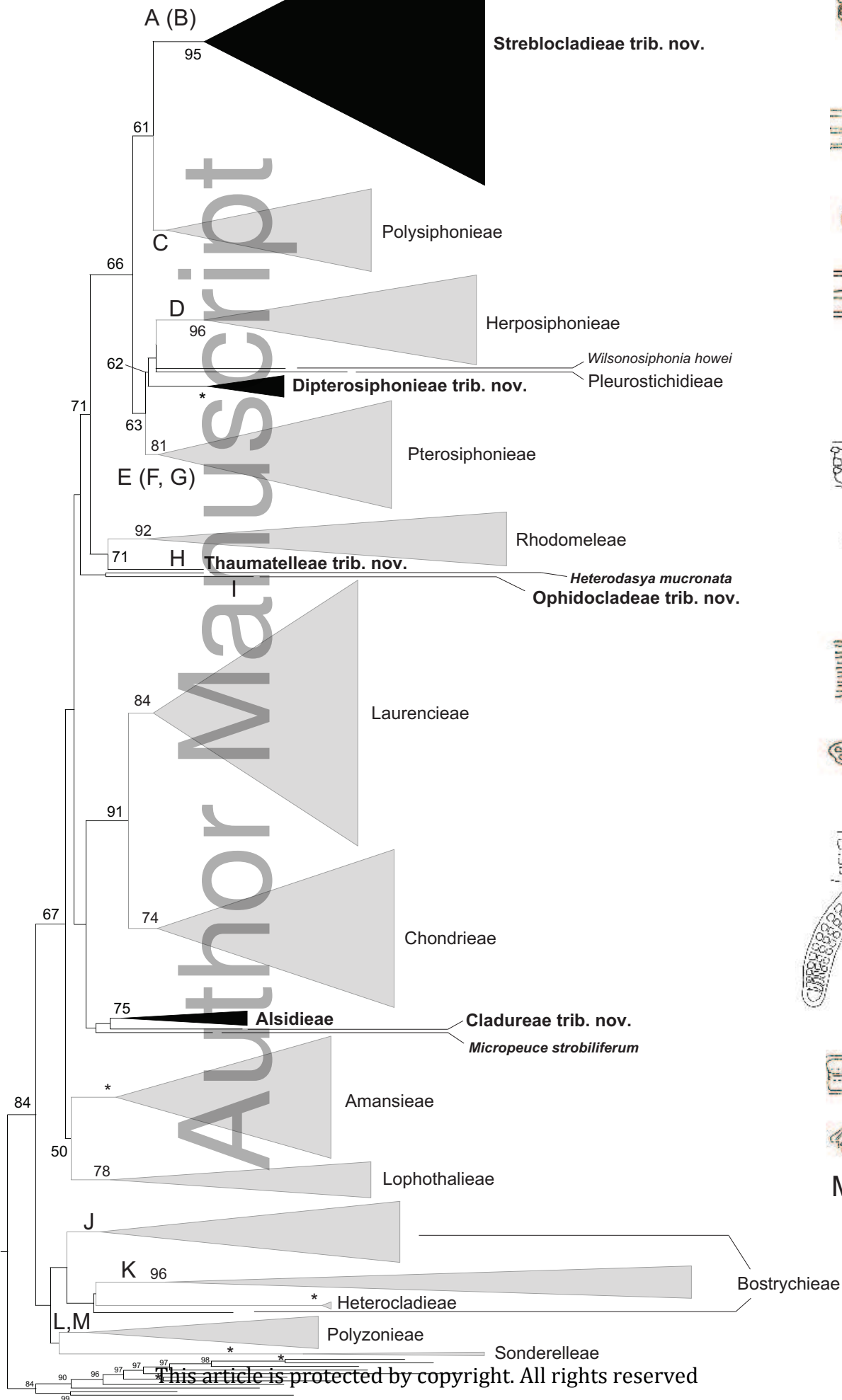1313   bootstrap support (*), except those where bootstrap values are indicated on branches.

1314   F<small>IG</small>. 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 *rbc*L, 179 18S rRNA gene and 194 *cox*1 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   F<small>IG</small>. 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   F<small>IG</small>. S2. Phylogeny of the family Rhodomelaceae. The RAxML tree used the genome-

1332   scale phylogeny based on nucleotides as a constraint and incorporated 322 *rbc*L, 179

1333   18S rRNA gene and 194 *cox*1 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.

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A (B)
95
Streblocladieae trib. nov.
61
C
Polysiphonieae
66
D
Herposiphonieae
96
62
Wilsonosiphonia howei
Dipterosiphonieae trib. nov.
Pleurostichidieae
*
63
81
Pterosiphonieae
E (F, G)
71
92
Rhodomeleae
71
H
Thaumatelleae trib. nov.
I
Heterodasya mucronata
Ophidocladeae trib. nov.
84
Laurencieae
91
74
Chondrieae
75
Alsidieae
Cladureae trib. nov.
Micropeuce strobiliferum
*
Amansieae
84
50
78
Lophothalieae
J
K
96
Bostrychieae
*
Heterocladieae
L,M
Polyzonieae
Sonderelleae
*
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Author/s:
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