

## Manuscript Details

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### Abstract

The order Ceramiales contains about one third of red algal diversity and it was classically classified into four families according to morphology. The first phylogenies based on one or two molecular markers were poorly supported and failed to resolve these families as monophyletic. Nine families are currently recognized, but relationships within and among them are poorly understood. We produced a well-resolved phylogeny for the Ceramiales using plastid genomes for 80 (27 newly sequenced) representative species of the major lineages. Three of the previously recognized families were resolved as independent monophyletic lineages: Ceramiaceae, Wrangeliaceae and Rhodomelaceae. By contrast, our results indicated that the other six families require reclassification. We propose the new order Inkyuleeales, a new circumscription of the Callithamniaceae to include the Spyridiaceae, and a new concept of the Delesseriaceae that includes the Sarcomeniaceae and the Dasyaceae. We also investigated the evolution of the thallus structure, which has been important in the classical delineation of families. The ancestor of the Ceramiales was a monosiphonous filament that evolved into more complex morphologies several times independently during the evolutionary history of this hyperdiverse lineage.

<b>Keywords</b>	Evolution; Morphology; New order; New subfamily; Phylogenomics; Rhodophyta
<b>Taxonomy</b>	Taxonomy, Systematics, Omics, Biological Classification, Evolutionary Biology, Phylogenetics
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Editors of the *Molecular Phylogenetics and Evolution*

Please find the manuscript entitled “Morphological evolution and classification of the red algal order Ceramiales inferred using chloroplast phylogenomics” by Pilar Díaz-Tapia, Marisa M. Pasella, Heroen Verbruggen & Christine A. Maggs, to be evaluated for publication in *Molecular Phylogenetics and Evolution*.

This paper presents the first comprehensive molecular phylogeny for the order that includes one third of the red algal diversity, the Ceramiales. We used 92 chloroplast genomes (28 newly determined) in order to resolve the phylogenetic relationships among major lineages of the order. Based on these phylogenies and morphological evidence, we reassessed the family level classification of the order, proposing a new order and merging four families in two. We also investigated the evolution of the thallus structure, which has been important in the classical delineation of families.

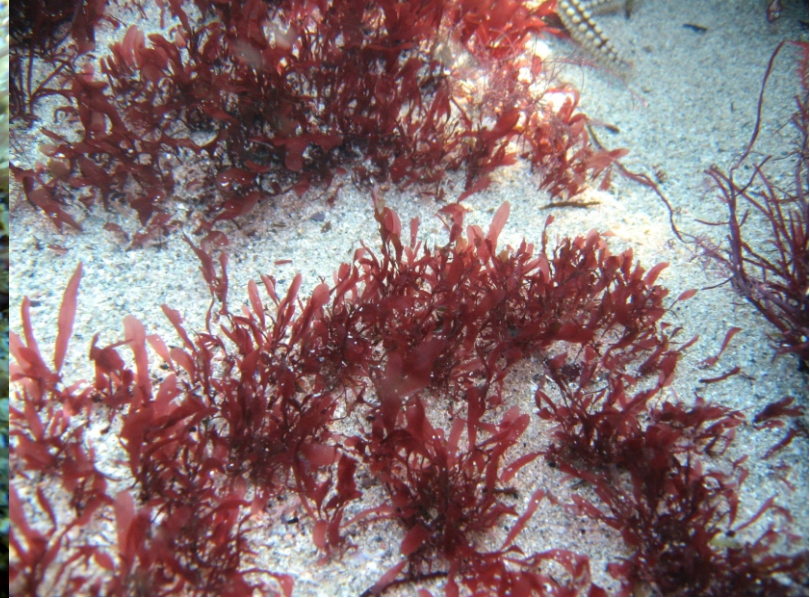
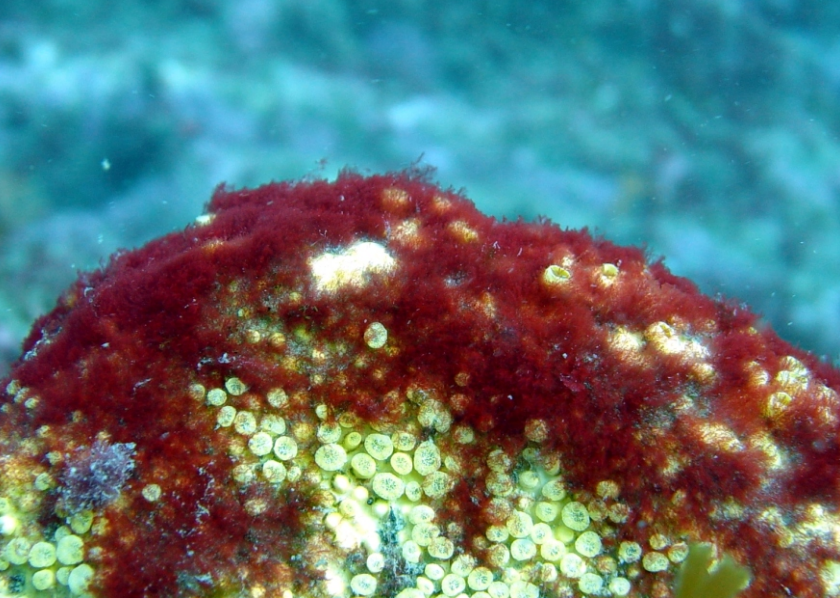
Besides the relevance of the results for the taxonomy of the Ceramiales and the red algae, we believe the work also has the potential to be an exemplary study of the use of massive HTS datasets in algal taxonomy. The highly conclusive results resulting from our dataset may inspire other systematists to use our approach to answer similar questions in their taxon of study.

We look forward to hearing from you.

Yours faithfully,

## Highlights

- Plastid phylogenomics resolves relationships among families in the Ceramiales
- Complex morphologies evolved multiple times from simple morphologies
- The Ceramiaceae, Wrangeliaceae and Rhodomelaceae are monophyletic
- The Spyridiaceae is subsumed into the Callithamniaceae
- The Sarcomeniaceae and Dasyaceae are subsumed into the Delesseriaceae



1 Morphological evolution and classification of the red algal order Ceramiales inferred  
2 using plastid phylogenomics

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19

20 ABSTRACT

21 The order Ceramiales contains about one third of red algal diversity and it was  
22 classically classified into four families according to morphology. The first phylogenies  
23 based on one or two molecular markers were poorly supported and failed to resolve  
24 these families as monophyletic. Nine families are currently recognized, but relationships  
25 within and among them are poorly understood. We produced a well-resolved phylogeny  
26 for the Ceramiales using plastid genomes for 80 (27 newly sequenced) representative  
27 species of the major lineages. Three of the previously recognized families were resolved  
28 as independent monophyletic lineages: Ceramiaceae, Wrangeliaceae and  
29 Rhodomelaceae. By contrast, our results indicated that the other six families require  
30 reclassification. We propose the new order Inkyuleeales, a new circumscription of the  
31 Callithamniaceae to include the Spyridiaceae, and a new concept of the Delesseriaceae  
32 that includes the Sarcomeniaceae and the Dasyaceae. We also investigated the evolution  
33 of the thallus structure, which has been important in the classical delineation of families.  
34 The ancestor of the Ceramiales was a monosiphonous filament that evolved into more  
35 complex morphologies several times independently during the evolutionary history of  
36 this hyperdiverse lineage.

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39 *Keywords:* Evolution; Morphology; New order; New subfamily; Phylogenomics;

40 Rhodophyta

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## 43 **1. Introduction**

44 The order Ceramiales, with 2,689 species currently recognized, accounts for more than  
45 a third of red algal species diversity (Guiry and Guiry, 2019). The Ceramiales is  
46 morphologically defined by details of its anatomy (the uniaxial thallus structure, the  
47 presence of periaxial cells and the post-fertilization formation of the auxiliary cell  
48 directly from the supporting cell) (Maggs and Hommersand, 1993; Womersley, 1998).  
49 Nägeli (1847) first named the order Ceramiales, and the earliest family level  
50 classification into Ceramiaceae, Delesseriaceae and Rhodomelaceae was proposed by  
51 Oltmanns (1904). Subsequently, the family Dasyaceae was segregated from the  
52 Rhodomelaceae (Rosenberg, 1933). These families were defined based on a  
53 combination of vegetative and reproductive characters (Kylin, 1956; Womersley, 1998;  
54 2003; Hommersand, 1963; Maggs and Hommersand, 1993). The Ceramiaceae form  
55 monosiphonous filaments (Fig. 1A, see the Glossary in supplementary data 1) and,  
56 when present in vegetative structures, the periaxial cells only cover parts of the axial  
57 cells. The Rhodomelaceae has a polysiphonous structure (the periaxial cells cover the  
58 full length of the axial cells) with axes developing monopodially (Fig. 1B-C, see Fig.  
59 S1A and the Glossary in supplementary data 1). The Dasyaceae also has a  
60 polysiphonous structure, but axes develop sympodially (Fig. 1H-I, see Fig. S1B and the  
61 Glossary in supplementary data 1) and bear unusual pigmented monosiphonous  
62 branches. The Delesseriaceae includes blade-like species that consist of polysiphonous  
63 axes in which the lateral periaxial cells divide to form the blade (Fig. 1L-M). These  
64 basic structures define the respective families, but in some representatives have evolved  
65 into networks of filaments (Fig. 1F), corticate terete (Fig. 1H) or blades (Fig. 1J-K), and  
66 parasites (Fig. 1G). In general, members of these families are easily recognized based  
67 on the thallus structure. However, some species or groups of species exhibit characters

68 interpreted as “intermediate” between several families. For example, *Halydictyon* has  
69 been considered to be related to the Delesseriaceae, Dasyaceae and the Rhodomelaceae  
70 (Womersley, 2003, as *incertae sedis*), *Sonderella* has been included in the  
71 Rhodomelaceae and the Delesseriaceae (Womersley, 1965) and the “*Sarcomenia* group”  
72 has morphological similarities with the Rhodomelaceae and Delesseriaceae and was  
73 finally segregated into the new family Sarcomeniaceae (Womersley and Shepley, 1959;  
74 Womersley, 2003).

75         The classification of the Ceramiales into five families based on morphology was  
76 maintained until the first molecular phylogenies including members of several families  
77 were constructed based on 18S rRNA gene sequences (Choi et al., 2002, 2008). These  
78 phylogenies resolved some lineages with high support, but they did not correspond with  
79 the previously established families. The Rhodomelaceae was the only taxon  
80 unequivocally resolved as monophyletic in these phylogenies. By contrast, other  
81 families were split into several clades and relationships among them remained  
82 unresolved. Based on these poorly supported phylogenies for the Ceramiales, four  
83 families were segregated for the Ceramiaceae (Callithamniaceae, Wrangeliaceae,  
84 Spyridiaceae and Inkyuleeaceae) (Choi et al., 2008). The Dasyaceae was divided into  
85 two subfamilies: the Dasyoideae and the Heterosiphonioideae (Choi et al., 2002).  
86 Likewise, in the Delesseriaceae, based on LSU and *rbcL* phylogenies, three subfamilies  
87 were recognized: Phycodryoideae, Nitophylloideae and Delesserioideae (Lin et al.,  
88 2001). Of these, only the Phycodryoideae was fully supported, while the other two  
89 subfamilies were not resolved as monophyletic in all analyses. These studies clearly  
90 indicate that better resolved phylogenies are needed to improve our understanding of  
91 phylogenetic relationships among the major lineages of Ceramiales and arrive at a stable  
92 classification.



93           The Ceramiales includes a high diversity of morphological structures that makes  
94 it a good candidate model for evolutionary studies. The structure of the female  
95 apparatus and post-fertilization development have been classically used in the  
96 Ceramiales and other red algae as key characters to infer relationships and establish a  
97 classification (Falkenberg, 1901; Rosenberg, 1933; Hommersand, 1963; Kylin, 1956;  
98 Díaz-Tapia and Bárbara, 2011). Their uniformity within major groups and the  
99 variability among them has been confirmed in phylogenetic analyses (Saunders and  
100 Hommersand, 2004; Choi et al., 2008; Yang et al., 2016). By contrast, the evolutionary  
101 patterns of vegetative structures in the Ceramiales have barely been discussed.  
102 Hommersand (1963) proposed that the ancestor of the order was a monosiphonous  
103 filamentous species that gave rise to two major monosiphonous lineages differing in  
104 branching pattern and the female structures. According to Hommersand (1963), eight  
105 lineages evolved independently from one of these two lineages: their morphologies  
106 maintained this basic structure or evolved into more complex types of thalli.

107           High throughput sequencing (HTS) techniques allow us to sequence complete  
108 organellar genomes and their potential usefulness in resolving challenging phylogenies  
109 has been demonstrated in several groups of animals and plants (e.g. Kocot et al., 2018;  
110 Sun et al., 2018). These tools have also successfully been applied in the resolution of  
111 difficult phylogenies in the red algae (Costa et al., 2016; Díaz-Tapia et al., 2017; Iha et  
112 al. 2018; Saunders et al., 2018; Pasella et al. 2019). Therefore, phylogenomic  
113 approaches could contribute to the construction of a well-supported phylogeny for the  
114 Ceramiales, providing a basis for reassessing its classification. The objective of this  
115 paper is to produce a molecular phylogeny for the order Ceramiales based on plastid  
116 genome data for representative taxa of the main clades of the order and suitable  
117 outgroups. We aim to reassess the classification of the Ceramiales based on joint

118 interpretation of this phylogeny and morphological characters relevant to the delineation  
119 of families. Furthermore, we aim to understand the evolution of thallus structure, on  
120 which the current classification of the Ceramiales has been established.

121

## 122 **2. Material and methods**

### 123 *2.1. Taxon sampling*

124 To identify the main lineages of the order Ceramiales, we considered previously  
125 published phylogenies, as well as the most recent proposed classifications based on  
126 molecular data (Lin et al., 2001; Choi et al., 2002, 2008; Díaz-Tapia et al., 2017; Table  
127 S1). An additional classification was published recently (Athanasiadis, 2016), but it  
128 does not include molecular phylogenetic analyses and several proposals are  
129 questionable because they are in stark contrast with what we know from molecular  
130 work. We selected one to four species of each major lineage for phylogenomic analyses.  
131 Plastid genomes are available in GenBank for 64 species of the Ceramiales, mostly in  
132 the family Rhodomelaceae (Díaz-Tapia et al., 2017; Pasella et al., 2019; Salomaki and  
133 Lane, 2019). In order to balance the number of taxa for the Ceramiales lineages, we  
134 excluded from our analyses 12 of the previously published genomes (ten  
135 Rhodomelaceae and two *Membranoptera* species) so that major lineages were  
136 represented by one to four species. Furthermore, we selected 28 additional species of  
137 the order Ceramiales to be newly analysed using high-throughput sequencing. Our  
138 taxon selection includes representative species of the type genera for all the families or  
139 subfamilies, with the exception of the subfamilies Phycodryoideae and  
140 Heterosiphonieae and the family Sarcomeniaceae. However, representative species  
141 included in our analyses for the Phycodryoideae and Heterosiphonieae were

142 unequivocally placed in the same lineages as their respective type genera (Lin et al.,  
143 2001; Choi et al., 2002, 2008). For the Sarcomeniaceae we included two genera in our  
144 taxon selection whose relationship with *Sarcomenia* has not been studied using  
145 molecular tools. However, we constructed an *rbcL* tree (not shown) including  
146 *Sarcomenia*, *Platysiphonia* and other related species according to our results and they  
147 formed a highly supported clade (98%). Our outgroup selection included 12 species  
148 representative of the red algal orders most closely related to the Ceramiales  
149 (Verbruggen et al. 2010; Yang et al. 2016). Plastid genomes of three of them were  
150 newly determined here.

151

## 152 *2.2. Data collection*

153 Total DNA was isolated with an adapted cetyltrimethylammonium bromide (CTAB)  
154 protocol (Doyle and Doyle, 1987) as described in Cremen et al. (2016). Barcoded  
155 sequencing libraries (350 nt) of the 27 DNA extracts were prepared with the TruSeq  
156 DNA HT Sample preparation Kit (Illumina, USA). Because the Verbruggen lab carries  
157 out organellar genome projects for red and green algae, we pooled DNA extracts of red  
158 and green algae prior to library preparation, resulting in reduced costs, and the  
159 assembled genomes were separated using bioinformatics (e.g. Costa et al., 2016; Díaz-  
160 Tapia et al., 2017). Libraries were sequenced on Illumina Hiseq X platform, generating  
161 150 nt paired-end reads. Assembly and annotation of the genomes were performed as  
162 previously described (Verbruggen and Costa, 2015; Marcelino et al., 2016). GenBank  
163 accession numbers for annotated genomes are provided in Table S2.

## 164 *2.3. Sequence alignment and phylogenetic analyses*

165 We assembled a dataset consisting of 92 plastid genomes: the 28 newly sequenced for  
166 the order Ceramiales, 52 previously published for the order Ceramiales, and 12  
167 genomes for other Rhodymeniophycidae to be used as outgroups (Table S2).  
168 In total, 208 protein-coding genes were aligned at the amino-acid level using  
169 MAFFT v7.245 (Kato and Standley, 2013) using default settings and checked visually  
170 in Geneious 6.1.7. Nucleotide alignments were constructed based on the inferred amino-  
171 acid alignments using TranslatorX (Abascal et al., 2010). Alignments were then  
172 concatenated and phylogenetic trees inferred with maximum likelihood (ML) in  
173 RAxML v8.0.26 (Stamatakis, 2014) with GTR+ $\Gamma$  and WAG+ $\Gamma$  models for the  
174 nucleotide and amino-acid alignments, respectively, using 100 traditional bootstrap  
175 replicates (Felsenstein, 1985). Further analyses were carried out to assess the sensitivity  
176 of these analyses to model choice (LG, CPREV).

#### 177 *2.4. Analysis of trait evolution*

178 Species were classified into seven morphological groups that represent the thallus  
179 structure in the order Ceramiales. These groups are 1) monosiphonous filaments  
180 (filaments formed by a single cell row, Fig. 1A), 2) polysiphonous filaments (filaments  
181 formed by an axial cell row surrounded by periaxial cells that cover partially or  
182 completely the axial cells, with periaxial cells producing a row of flanking cells in some  
183 species, Fig. 1B-E), 3) corticate terete (corticate polysiphonous filaments, in which the  
184 cortication covers more than 70% of the thallus and medullary and cortical layers are  
185 distinguishable in cross sections, Fig. 1H-I), 4) membranous blades (blades formed by a  
186 layer of cells, Fig. 1L-M), 5) blades formed by a network of filaments (blade-like  
187 species composed of axial filaments with monosiphonous branches that fuse to form a  
188 network, Fig. 1F), 6) thick leathery (corticate blades, Fig. 1J-K), and 7) parasites (Fig.  
189 1G).

190 Trait evolution analyses were carried out in R 3.3.2 (R Core Team, 2013), using the  
191 *geiger* and *phytools* packages (Harmon et al., 2008; Revell, 2011). Equal rates (ER),  
192 symmetrical, all rates different and a user-defined model were fitted and compared with  
193 the AICc criterion. The user-defined model is a variant of the equal rates model in  
194 which some biologically implausible transitions are disallowed, i.e. transitions from  
195 parasite to non-parasite, from blade and leathery to monosiphonous, and from  
196 monosiphonous directly to blade and leathery. Ancestral state estimation was carried  
197 out with the *make.simmap* function in *phytools* using 100 simulations, and the ER and  
198 user-defined model.

199

### 200 **3. Results**

#### 201 *3.1. Phylogenetic relationships and classification*

202 Among the newly assembled genomes, seven were complete, eight could not be  
203 confirmed as circular but we recovered all or nearly all the genes for them, and 13 were  
204 partial (see Table S2). Moreover, we determined three complete genomes of other  
205 Rhodymeniophycidae to be used as outgroups (Table S2). Our analyses also included 52  
206 plastid genomes of the Ceramiales and nine of other Rhodymeniophycidae that were  
207 downloaded from GenBank (Table S2). A concatenated alignment of 92 species and  
208 208 genes, amounting to 160,464 nucleotides or 53,488 amino acid positions, was  
209 analysed.

210         Plastid phylogenomics resolved the relationships among the major lineages of  
211 the Ceramiales with full support for the vast majority of branches (Fig. 2). The topology  
212 was robust to analysing the data as nucleotides or amino acids (Fig. 2 vs. S3). Only five  
213 branches received bootstrap support lower than 85.

214 The core of the Ceramiales was resolved in a monophyletic group that received  
215 full support. *Inkyuleea* is the only taxon currently assigned to the Ceramiales that was  
216 not placed within this clade. Conversely, it was resolved with high support as sister to  
217 *Schimmelmannia* of the order Acrosymphytales. *Inkyuleea* includes three species and is  
218 the only genus of the family Inkyuleeaceae.

219 The core of the Ceramiales contains five major clades. The families  
220 Ceramiaceae, Wrangeliaceae and Rhodomelaceae were monophyletic and received full  
221 or high support. The Callithamniaceae, including *Spyridia* (at present in the  
222 Spyridiaceae), formed a clade with very high statistical support (97). The families  
223 Dasyaceae and Delesseriaceae as currently delineated were not resolved as  
224 monophyletic. The clade indicated as Delesseriaceae in our phylogeny was fully  
225 supported and was composed of species previously assigned to the families  
226 Sarcomeniaceae, Dasyaceae and Delesseriaceae. Within this clade, six lineages are  
227 distinguished, of which five correspond to the subfamilies of the Delesseriaceae  
228 (Delesserioideae, Phycodryoideae and Nitophylloideae) and Dasyaceae (Dasyoideae  
229 and Heterosiphonoideae). The sixth lineage is proposed as the new subfamily  
230 Sarcomenioideae and includes *Malaconema* and *Platysiphonia* (former  
231 Sarcomeniaceae), as well as *Apoglossum*, *Caloglossa*, *Taenioma* (formerly in the  
232 Delesserioideae) and *Halydictyon* (formerly *incertae sedis*).

233

### 234 3.2. Evolution of the thallus structure

235 The trait evolution analyses indicated that the less parameter-rich models equal rates  
236 (ER) and custom models outperformed the more parameter-rich symmetric (SYM) and  
237 all rates different (ARD) models based on the uncorrected and corrected Akaike

238 Information Criteria (AIC and AICc, Table 1). The ancestral character estimation  
239 indicated that the ancestor of the Ceramiales was a monosiphonous filamentous species  
240 (Figs 3 and S4) and this condition is present in the earliest diverged lineages of the  
241 order. Polysiphonous filaments, corticated terete, blade-like and leathery thalli, and  
242 networks of filaments evolved in independent lineages several times in the evolution of  
243 the Ceramiales. Only the plastid genome of one parasitic species was available at the  
244 time of writing, but parasites are known in multiple lineages of the family and this  
245 condition also evolved multiple times independently in the Ceramiales. The ancestral  
246 state estimation using the custom rate matrix (Fig. 3) and equal rates (Fig. S4) models  
247 produced similar results. The main difference between them is that the common  
248 ancestor of the Rhodomelaceae and Delesseriaceae was resolved, respectively, as  
249 polysiphonous or with high likelihoods of being blade-like.

250

#### 251 **4. Discussion**

252 Our analyses of plastid genomes provide the first well-resolved phylogeny for the order  
253 Ceramiales. This is an important step forward in understanding the evolution and  
254 classification of this order that accounts for one third of red algal diversity (Guiry and  
255 Guiry, 2019). It contrasts with previous phylogenies based on one or a few molecular  
256 markers that failed to resolve relationships among most lineages (Lin et al., 2001; Choi  
257 et al., 2002, 2008). Our phylogeny is used to reassess family level classification and to  
258 analyse the evolution of thallus structure in this order.

259

##### 260 *4.1. Phylogenetic relationships and classification*

261 *Inkyuleea* was resolved in our phylogeny as sister to *Schimmelmannia* (order  
262 Acrosymphytales). Accordingly, we propose the erection of the new order Inkyuleeales.  
263 Its segregation from the Ceramiales has been suggested before but was not formally  
264 proposed due to uncertainties about its phylogenetic relationships with other red algae  
265 (Choi et al., 2008). The segregation of this new order is also supported by its  
266 morphological characters. The thallus structure of *Inkyuleea* resembles the Ceramiales,  
267 but the post-fertilization development of gonimoblasts includes the formation of an  
268 auxiliary branch on the supporting cell (Wollaston, 1974). This character resembles the  
269 auxiliary branches formed in the Acrosymphytales (Saunders et al., 2016) and differs  
270 from the single auxiliary cell produced in the Ceramiales (Wollaston, 1974). Other  
271 vegetative and reproductive characters that differ between the Inkyuleeales and  
272 Acrosymphytales include isomorphic vs. heteromorphic life histories, with crustose  
273 tetrasporophytes in the latter (Withall and Saunders, 2007; Saunders et al., 2016).

274 Earlier molecular phylogenies of the Ceramiaceae led to its division into four  
275 families (plus the Inkyuleeaceae, discussed above) (Choi et al., 2002, 2008). However,  
276 our phylogeny resolved them in three independent clades corresponding to the  
277 Ceramiaceae, Wrangeliaceae and Spyridiaceae/Callithamniaceae. The last two families  
278 were unequivocally resolved as sister, leading to our proposal for their merger into a  
279 single family, the Callithamniaceae having priority. The Spyridiaceae contains a single  
280 free-living genus with 15 species, characterized by distinctive vegetative and  
281 reproductive structures, and its placement in the Ceramiales has even been questioned  
282 (Choi et al., 2008). However, Hommersand (1963) confirmed its relationship with the  
283 tribes Crouanieae and Callithamnieae (both in the Callithamniaceae) based on several  
284 morphological features, including a synapomorphy: the complete absence of sterile cells  
285 in the procarps of the female apparatus. The Ceramiaceae and Wrangeliaceae were



286 supported in our phylogeny, which resolved all the available representatives of these  
287 families in two independent clades. These two families were delineated based on a  
288 combination of vegetative and reproductive characters by Choi et al. (2008) with a  
289 special emphasis on the position and structure of the procarps. Relationships among  
290 genera, and implicitly among tribes, within each family differed considerably with  
291 respect to previous phylogenies (Choi et al., 2008). For example, *Wrangelia* (tribe  
292 Wrangelieae) was resolved in our tree as sister to *Plumaria* (tribe Ptiloteae), while it  
293 was placed as sister to the Griffithsieae in previous phylogenies (Choi et al., 2008). Our  
294 phylogeny shows that the tribe Griffithsieae needs reassessment. *Bornetia* is currently  
295 included in that tribe (Athanasiadis, 1996), but it forms a clade with members of the  
296 Spermothermiae (*Spermothermion*, *Ptilothermion*) and Sphondylothermiae  
297 (*Sphondylothermion*); the Griffithsieae (represented by *Anotrichium* in our tree) is sister  
298 to the clade formed by the Compsothermiae (*Compsothermion*) and the  
299 Spongocloniae (*Pleonosporium*). The Wrangelieae, Ceramiaceae and  
300 Callithamniaceae include 926 species in 141 genera and 29 tribes. Their classification is  
301 mainly based on morphological characters, while phylogenetic relationships have been  
302 scarcely studied.

303 Our phylogenomic analyses show that the Dasyaceae and Delesseriaceae as  
304 previously circumscribed are paraphyletic and require re-classification, confirming  
305 previous indications based on single marker phylogenies (Choi et al., 2002). Members  
306 of these two families together with the Sarcomeniaceae are placed in our phylogeny in a  
307 fully supported clade. The classification adopted after the publication of the first  
308 molecular phylogenetic analyses subdivided the Delesseriaceae and Dasyaceae into five  
309 subfamilies (Lin et al., 2001; Choi et al., 2002). Four of these subfamilies were  
310 supported in our phylogeny and they were morphologically characterized in previous

311 works (Lin et al., 2001; Choi et al., 2002; Wynne, 2013). However, some genera  
312 currently included in the Delesserioideae (*Caloglossa*, *Taenioma*, *Apoglossum*) were  
313 resolved in a lineage not closely related to the type genus of the subfamily in a clade  
314 with species of the Sarcomeniaceae and *Halydictyon* (*incertae sedis*, Womersley, 2003).  
315 This result is unsurprising considering that the alliance between these genera and the  
316 Delesserioideae was previously unsupported (Lin et al., 2001; Choi et al., 2002).  
317 Therefore, our results demonstrate the necessity of taxonomic revision and we propose  
318 to merge the three families, the Delesseriaceae having priority. The current subfamilial  
319 classification is maintained and the Sarcomenioideae is recognized as a subfamily that  
320 also includes the genera *Caloglossa*, *Taenioma*, *Apoglossum* and *Halydictyon*. We also  
321 propose the new tribe Halydictyae for the genus *Halydictyon*, which differs from other  
322 Ceramiales by unusual morphological characters (Womersley, 2003).

323         The Delesseriaceae and Rhodomelaceae were resolved as sister families in our  
324 phylogeny, an alliance that had been previously suggested based on their morphological  
325 similarities (Rosenberg, 1933; Hommersand, 1963). They share a polysiphonous  
326 structure that in some lineages evolved into a foliose thallus, have a uniform procarp  
327 structure, and the gonimoblast is surrounded by a pericarp. In general, the majority of  
328 representatives from both families are easily distinguishable by their thallus structure.  
329 However, both are highly diverse groups (ca. 500 and 1000 species, respectively) and  
330 several of the characters that are typical for one of the families are not present in all the  
331 members or are also present in a few members of the other family. For example,  
332 trichoblasts (unpigmented monosiphonous apical branches) are exclusive to the  
333 Rhodomelaceae, but some species lack them. The periaxial cells are formed by circular  
334 or alternate divisions in the Rhodomelaceae and Delesseriaceae, respectively, but  
335 alternate divisions are also present in some Delesseriaceae (some Sarcomenioideae).

336 The high morphological diversity within each family makes it difficult to establish a  
337 universal delineation. Still, there are synapomorphies in the Delesseriaceae as here  
338 redefined and the Rhodomelaceae related to the development of the carposporophyte: 1)  
339 the auxiliary cell produces a single gonimoblast initial in the Rhodomelaceae, while it  
340 divides transversely forming several gonimoblast initials in the Delesseriaceae; and 2)  
341 the gonimoblast is monopodially branched in the Delesseriaceae, while in the  
342 Rhodomelaceae it branches sympodially (Rosenberg, 1933; Hommersand, 1963).

343

#### 344 *4.2. Selection of taxonomic ranks*

345 Alternatives to our proposed classification of the Ceramiales and the  
346 Delesseriaceae clade are possible. One of them would consist of raising the five  
347 subfamilies of the former Delesseriaceae and Dasyaceae to the family level, maintaining  
348 the Sarcomeniaceae. A second alternative would be raising the five families we are  
349 recognizing to ordinal level, reorganizing the lower taxonomic levels (subfamilies and  
350 tribes). Most current classifications combine classical phenotypic observations with  
351 phylogenies to establish taxonomic levels (Avisé and Johns, 1999). Accordingly, we  
352 delineated the family Delesseriaceae based on its forming a neatly defined clade that  
353 can be characterized by synapomorphic morphological characters. Taxonomic ranks are  
354 arbitrary and, when taxa are considered individually, the attributed rank does not alter  
355 the interpretation of the information they provide about characters and systematic  
356 relationships (Avisé and Johns, 1999; Giribet et al., 2016; Kraichak et al., 2017).  
357 However, this can be a source of bias when establishing comparisons among distant  
358 taxa or when using taxonomic surrogacy, i.e. using counts of families or genera to  
359 measure biodiversity (Kraichak et al., 2017; Sigwart et al., 2017).

360 Our proposed classification for the Ceramiales includes families that are in turn  
361 subdivided into tribes, and moreover the Delesseriaceae has an intermediate taxonomic  
362 rank, subfamilies (Table S1), which might be actually equivalent to the tribes in other  
363 families. In the Delesseriaceae, both taxonomic ranks are needed, as they represent  
364 well-defined morphological groups and, when studied, they were supported in  
365 phylogenies (Lin et al., 2001; Choi et al., 2002; Wynne, 2013). The necessity for  
366 standardization of taxonomic ranks used in biological classification among organisms  
367 has been hotly debated (e.g. Avise and Johns, 1999; Giribet et al., 2016; Kraichak et al.  
368 2017). Temporal banding, i.e. the use of a standardized time of divergence for the  
369 assignment of taxonomic ranks, has been proposed as a universal system (Hennig, 1966;  
370 Avise and Johns, 1999). However, this method requires time-calibrated phylogenies,  
371 which are rare in the red algae probably because the fossil record is scarce and  
372 phylogenies are commonly difficult to resolve using few molecular markers. Further  
373 work is needed to evaluate whether the taxonomic ranking for the Ceramiales includes  
374 unequal ranks considering the divergence time of taxa.

375

#### 376 *4.3. Thallus structure evolution*

377 The ancestral state estimation suggests that the ancestor of the Ceramiales was a  
378 monosiphonous filamentous species, the simplest morphological architecture of the  
379 order. This agrees with previous interpretations based on morphology that proposed that  
380 the order derives from a primitive Ceramiaceae (Hommersand, 1963). The  
381 monosiphonous condition persists in the earliest diverged lineages of the Ceramiales  
382 (Ceramiaceae, Callithamniaceae and Wrangeliaceae). Other more complex thallus  
383 structures that characterize the extant Ceramiales displayed a complex evolutionary  
384 pattern. Polysiphonous filaments are thought to have evolved through a reduction of

385 whorled branches to single cells (Hommersand, 1963). According to our inferred  
386 ancestral states, this happened independently in three clades of the Ceramiales  
387 (Ceramiaceae, some Callithamniaceae, and Rhodomelaceae/Delesseriaceae).

388 Blade-like thalli evolved independently in the Rhodomelaceae and the  
389 Delesseriaceae. Developmentally, these thalli are thought to have evolved from  
390 polysiphonous filaments by the division of the lateral periaxial cells, leading to the  
391 formation of wings, or by the fusion of lateral branches (Womersley, 2003; Wynne,  
392 2013). The estimation of the ancestor of the Rhodomelaceae and Delesseriaceae differed  
393 between the analyses using custom rate matrix and equal rates models (polysiphonous  
394 or with high likelihoods of being blade-like respectively). Considering that a direct  
395 transition from monosiphonous to blade-like seems developmentally unlikely in the  
396 Ceramiales, we are of the opinion that the ancestral states inferred from the custom  
397 model are more realistic.

398 Blade-like thalli were inferred to have been ancestral to two lineages of  
399 Delesseriaceae that form networks of filaments by cell adhesion between branches.  
400 Corticate terete and leathery thalli are thought to have evolved by the development of a  
401 cortex covering the cylindrical or blade-like thalli in several lineages of the  
402 Wrangeliaceae, Delesseriaceae and Rhodomelaceae (Womersley, 1998, 2003; Wynne,  
403 2002, 2013), a hypothesis that is supported by our inferred ancestral states. Furthermore,  
404 a secondary reduction of the wings of blades occurred twice in the Delesseriaceae. It led  
405 to the formation of polysiphonous filaments in which a flanking row of cells still  
406 persists in all or part of the thallus (*Taenioma* and *Platysiphonia/Malacconema*)  
407 (Womersley, 2003, Wynne, 2013). Parasites have extremely reduced thalli and have  
408 evolved independently in multiple lineages of the Ceramiales (Preuss et al., 2017;  
409 Preuss and Zuccarello, 2019; Salomaki and Lane, 2019).

410           The evolution of thallus morphology from simple filaments to more complex  
411 structures implies a decrease in the thallus surface to volume ratio. High surface to  
412 volume ratios are correlated in extant seaweeds with rapid nutrient uptake and growth  
413 rates, which are higher in filamentous and blade-like species than in corticated terete  
414 and leathery species (Littler and Littler, 1980; Hurd et al., 2014). Therefore, the  
415 morphological diversification of thallus structures may have allowed the Ceramiales to  
416 also diversify into different ecological niches. Evolutionary drivers of morphological  
417 change in seaweeds are poorly understood, but it has been hypothesized that grazing  
418 pressure and CO<sub>2</sub> availability could have been involved in the morphological  
419 diversification during the Ediacaran (541-635 My) (Xiao and Dong, 2006). Similar  
420 drivers might be the underlying cause of the evolution of the Ceramiales, but a better  
421 understanding of environmental controls over development as well as more detailed  
422 insights into the timing of Ceramiales diversification will be needed to evaluate this  
423 hypothesis in more detail.

424

## 425 **5. Conclusions**

426           For the first time, the relationships of the Ceramiales are reconstructed in a well-  
427 supported phylogeny. This adds to the growing body of evidence that phylogenomics  
428 and transcriptomics can resolve challenging phylogenies in the red algae (Costa et al.,  
429 2016; Díaz-Tapia et al., 2017; Oliveira et al., 2018; Saunders et al., 2018; Pasella et al.,  
430 2019). Of the nine families currently recognized, three were supported as previously  
431 circumscribed. However, six families required reclassification. The families proposed in  
432 this work are distinguished by synapomorphic characters of the female structures or  
433 carposporophyte development. The thallus structure, however, which was traditionally  
434 used to distinguish the families, displayed complex evolutionary dynamics. Some

435 thallus types evolved multiple times in independent lineages of the family, leading to  
436 misinterpretations of the affinities among taxa. The thallus structure in the Ceramiales  
437 increased in complexity during its evolution from a monosiphonous filamentous  
438 ancestor, and this process is likely to be linked to niche differentiation.

439         In this work, we reassessed the family level classification of the Ceramiales based  
440 on a selection of 80 species representative of the previously recognized major lineages.  
441 However, a large number of genera and species of this order have never been  
442 investigated using molecular tools. Thus, further studies will be required to acquire a  
443 more comprehensive understanding of the Ceramiales and reassess their classification at  
444 lower taxonomic levels. Large knowledge gaps remain, particularly in the families  
445 Wrangeliaceae, Callithamniaceae and Ceramieae, which are probably the most  
446 understudied groups of the red algae although they contain almost 1,000 currently  
447 recognized species. This is in part due to a large proportion of species in these groups  
448 being small in size (< 5 mm) so their morphological and molecular study requires  
449 additional effort compared with larger red algae.

450

## 451 **6 Formal taxonomy**

452 Table S1 provides a summary of the family level classification of genera and tribes in  
453 the Ceramiales as a result of our work, as well as a comparison with the previous  
454 classification according to studies that included phylogenetic analyses. Below we  
455 provide descriptions for taxa that require emendation, as well as the new taxa.

### 456 *6.1. Inkyuleeales Díaz-Tapia & Maggs, ord. nov.*

457 Diagnosis: Thalli erect and uniaxial, consisting of uniseriate filaments with rhizoidal  
458 cortication in lower axes. Each axial cell bearing three whorl branchlets, one major

459 opposite two minor. Life history triphasic, with isomorphic gametophytes and  
460 tetrasporophytes. In female gametophytes, carpogonial branches are formed adaxially  
461 on basal cells of major branchlets. After fertilization, the supporting cell produces a 3-4-  
462 celled auxiliary branch and the subapical cell fuses with the carpogonium.

463 Type family: Inkyuleeaceae H.-G.Choi, Kraft & G.W.Saunders (2008, pp 1040-1041)

464

465 *6.2. Delesseriaceae Bory (1828, p. 181), fam. emend. Díaz-Tapia & Maggs*

466 Thalli foliose, terete or compressed, attached by rhizoids with multicellular haptera or a  
467 discoid fibrous rhizoidal holdfast. Structure uniaxial, growth through divisions of an  
468 apical cell that produces an axial filament whose cells divide longitudinally forming 4-  
469 11 periaxial cells. In the Delesserioideae, Nitophylloideae, Phycodryoideae and  
470 Sarcomenioideae the lateral periaxial cells undergo oblique divisions forming one or  
471 several orders of cell rows that produce a membrane or a row of flanking cells. In the  
472 Heterosiphonioideae and Dasyoideae the axial filament is clothed by pigmented  
473 monosiphonous branches. In *Halydictyon* (Sarcomenioideae), thallus consisting of a  
474 network of monosiphonous filaments. Spermatangia formed on the thallus surface or on  
475 monosiphonous branches. Procarps consisting of a supporting cell, a lateral sterile group  
476 of 1-7 cells, a four-celled carpogonial branch and a basal sterile group of 1-4 cells. The  
477 fertilized carpogonium cuts off two connecting cells of which one fuses with the  
478 auxiliary cell. The auxiliary cell produces several gonimoblast initials. Gonimoblasts  
479 monopodially branched and bearing carposporangia, cystocarps ostiolate.  
480 Tetrasporangia formed in sori or stichidia; tetrahedrally divided.

481 Type genus: *Delesseria* J.V.Lamouroux (1813, p. 122)

482



483 6.3. *Callithamniaceae* Kützing (1843, p. 370), fam. emend. Díaz-Tapia & Maggs

484 Thalli filamentous, uniaxial, with each axial cell bearing determinate or indeterminate  
485 branches that are arranged distichously, radially or in whorls. In female gametophytes,  
486 procarps are four-celled and sterile cells are completely absent. Gonimoglobes with or  
487 without sterile involucral cells.

488 Type genus: *Callithamnion* Lyngbye (1819, p. 123)

489

490 6.4. *Sarcomenioideae* Díaz-Tapia & Maggs, subfam. nov.

491 Thalli foliose, terete with flanking cells throughout the entire or part of the thallus or  
492 net-like in *Halydictyon*. Structure uniaxial, growth through divisions of an apical cell  
493 that produces an axial filament whose cells form a network (*Halydictyon*) or divide  
494 longitudinally forming four periaxial cells; the lateral periaxial cells undergo oblique  
495 divisions forming one to several orders of cells rows that produce a membrane or a row  
496 of flanking cells. Intercalary divisions in primary cell rows absent. In female  
497 gametophytes, procarps are restricted to primary cell rows, consisting of a four-celled  
498 carpogonial branch with two groups of sterile cells.

499 Type genus: *Sarcomenia* Sonder (1845, p. 56)

500

501 6.5 *Halydictyae* Díaz-Tapia & Maggs, trib. nov.

502 Thalli consisting of a network of monosiphonous filaments formed by the union of  
503 lateral cells. Fertile axes in female gametophytes producing four pericentral cells that  
504 bear a carpogonial branch. Spermatangial axes ovate and compressed, with sterile

505 marginal cells. Two tetrasporangia per segment are formed on compressed stichidia that  
506 consist of an axial cell and four pericentral cells.

507 Type genus: *Halydictyon* Zanardini (1843, p. 52)

508

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707

708 **Figure legends**

709

710 **Fig. 1.** Types of thallus structure in the Ceramiales. (A) Monosiphonous filament,  
711 *Antithamnionella ternifolia*. (B, C) Polysiphonous filament, in cross section (C) with an  
712 axial cell (a) surrounded by periaxial cells (p), *Polysiphonia scopulorum*. (D, E)  
713 Polysiphonous filament, in cross section (E) with an axial cell (a) surrounded by  
714 periaxial cells (p), and flanking cells (f) cut off from lateral periaxial cells, *Taenioma* sp.  
715 (F) Network of filaments, *Halydictyon mirabile*. (G) Parasite, *Choreocolax*  
716 *polysiphoniae* (arrow) on *Vertebrata lanosa*. (H, I) Corticate terete axes, in cross  
717 section (I) with an axial cell (a) surrounded by periaxial cells (p), a layer of medullary  
718 cells (m) and cortical cells (c), *Dasyphonia japonica*. (J, K) Leathery thalli, in cross  
719 section (K) with an axial cell (a) surrounded by periaxial cells (p), a layer of medullary  
720 cells (m) and cortical cells (c), *Alsidium seaforthii*. (L, M) Blade-like thalli, in cross  
721 section (L) with an axial cell (a) surrounded by pericentral cells (p) and a blade (b)  
722 formed by division of the lateral periaxial cells, *Cryptopleura ramosa*. Scale bars: 30  
723  $\mu\text{m}$  in Fig. A; 450 in Fig. B; 60  $\mu\text{m}$  in Fig. C; 200  $\mu\text{m}$  in Figs D, F and I; 75  $\mu\text{m}$  in Fig.  
724 E; 350  $\mu\text{m}$  in Fig. G; 8 mm in Fig. H; 2 cm in Fig. J; 300  $\mu\text{m}$  in Fig. K; 250  $\mu\text{m}$  in Fig.  
725 L; 1.5 cm in Fig. M.

726 **Fig. 2.** Phylogeny of the order Ceramiales indicating families and the order Inkyuleeales  
727 with light or dark shaded areas; the unshaded area corresponds to the outgroup. New  
728 taxa are indicated with bold font. RAxML tree based on nucleotide alignment of the 208  
729 concatenated genes from the plastid genome. All branches have full bootstrap support,  
730 except where bootstrap values are indicated on branches. In the Delesseriaceae bars  
731 show the subfamilial level classification and the former familial classification of each

732 species is indicated (DA = Dasyaceae, DE = Delesseriaceae, SA = Sarcomeniaceae, IS  
733 = *incertae sedis*).

734 **Fig. 3.** Ancestral character estimation for the thallus structure in the Ceramiales. Pie  
735 charts indicate proportion of reconstructed character histories under a user-defined  
736 model in which some transitions were disallowed.

737

738 Supplemental data 1. Glossary and Figs S1-2.

739 Supplemental Fig. S1. (A) *Vertebrata byssoides*, thallus with monopodial growth. (B)  
740 *Dasya gunniana*, thallus with sympodial growth. Images taken from Harvey (1847,  
741 1850).

742 Supplemental Fig. S2. *Rhodomela virgata*. Procarp and gonimoblast development. (A)  
743 Procarp consisting on a supporting cell (su), a sterile cell (st), and a carpogonial branch  
744 (1-3) bearing the carpogonium (cp). (B) After the fertilization, the supporting cell (su)  
745 produces an auxiliary cell (aux). (C) Cystocarp consisting on the gonimoblast (g)  
746 resulting from the divisions of the auxiliary cell that is surrounded by the pericarp (p).  
747 Images taken from Kylin 1956.

748

749

750 Supplemental Fig. S3. Phylogeny of the order Ceramiales indicating families and the  
751 order Inkyuleeales with light or dark shaded areas; the unshaded area corresponds to the  
752 outgroup. New taxa are indicated with bold font. RAxML tree based on amino acid  
753 alignment of the 208 concatenated genes from the plastid genome. All branches have  
754 full bootstrap support, except where bootstrap values are indicated on branches. In the  
755 Delesseriaceae bars show the subfamilial level classification and the former familial

756 classification of each species is indicated (DA = Dasyaceae, DE = Delesseriaceae, SA =  
757 Sarcomeniaceae, IS = *incertae sedis*).

758 Supplemental Fig. S4. Ancestral character estimation for the thallus structure in the  
759 Ceramiales. Pie charts indicate proportion of reconstructed character histories under an  
760 equal rates model.

761 Supplemental Table S1. Classification of genera and tribes of the Ceramiales in works  
762 including molecular data (excluding the Rhodomelaceae, see Díaz-Tapia et al. 2017).

763 Supplemental Table S2. GenBank accession numbers of the plastid genomes included in  
764 the phylogenetic analysis.

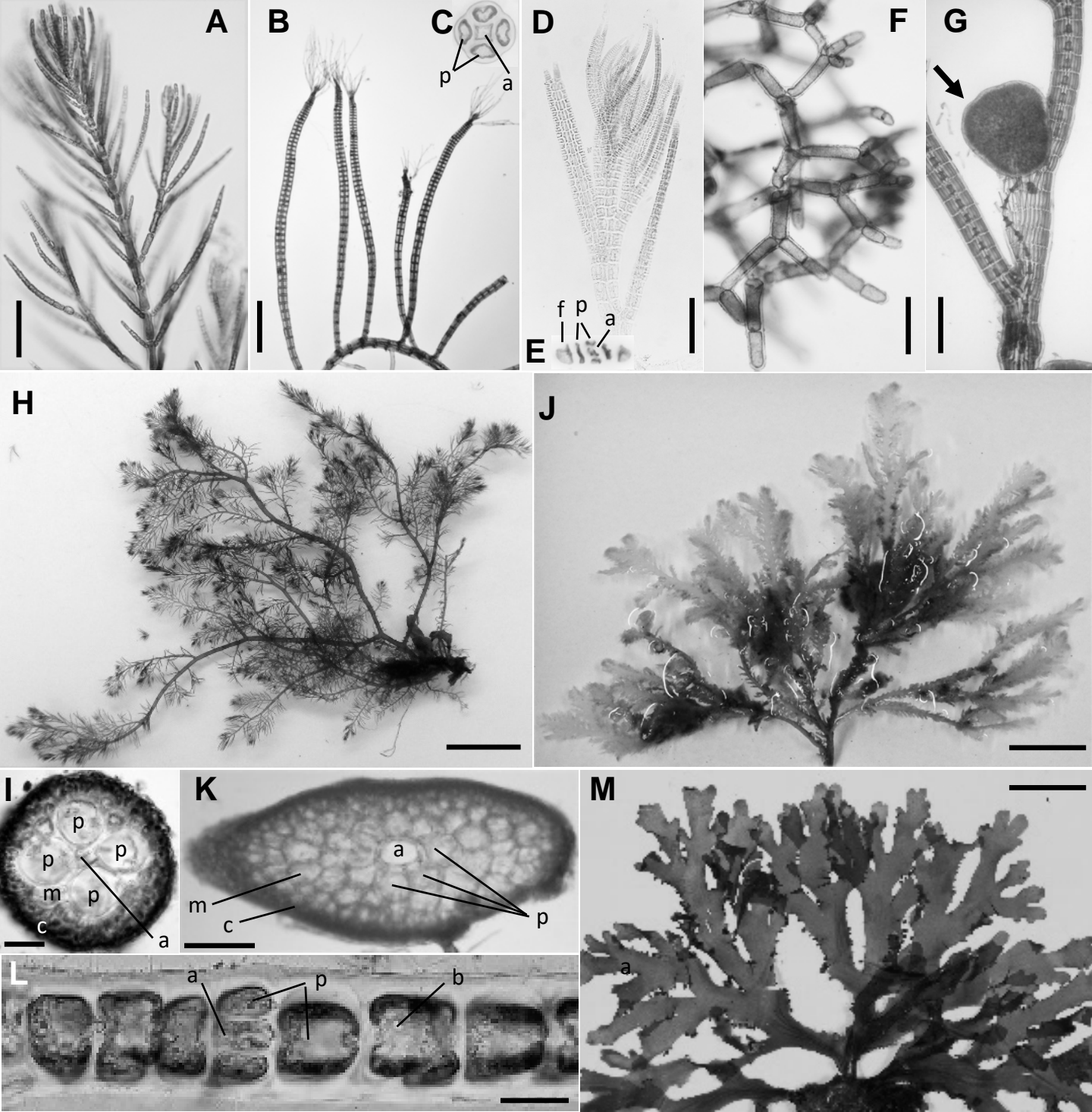
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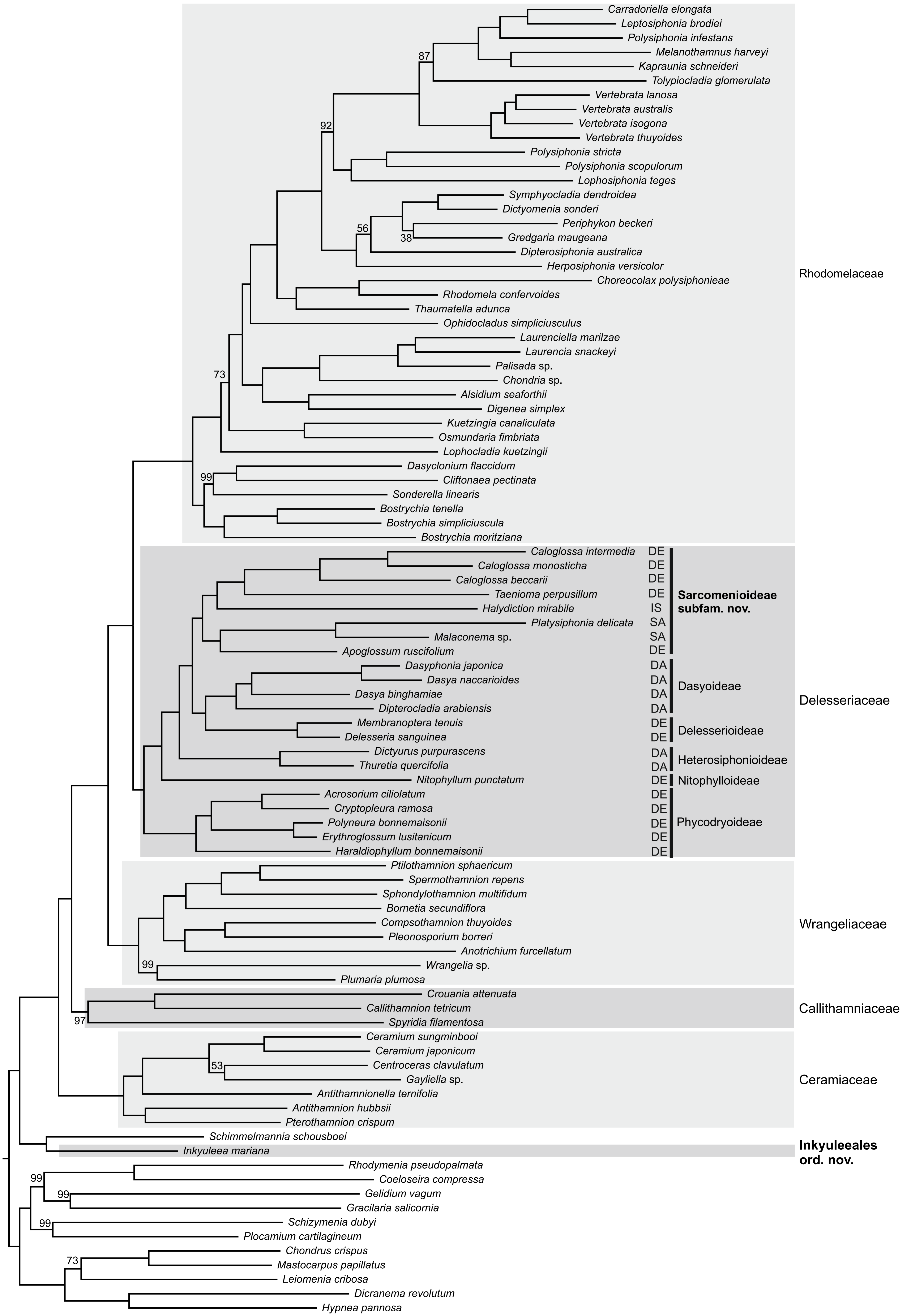
766 Table 1. Comparison of models of trait evolution showing that the parameter-rich  
767 symmetrical (SYM) and all rates different (ARD) models are outperformed (higher AIC  
768 and AICc) by the simpler equal rates (ER) and custom models. The log-likelihood is  
769 given under lnL, number of model parameters as k along with the uncorrected and  
770 sample-size corrected Akaike Information Criterion (AIC and AICc).

	lnL	k	AIC	AICc
ER	-97.28011	1	196.5602	196.6109
SYM	-85.51230	21	213.0246	228.6856
ARD	-79.35069	42	242.7014	337.7540
custom	-99.70025	1	201.4005	201.4511

771

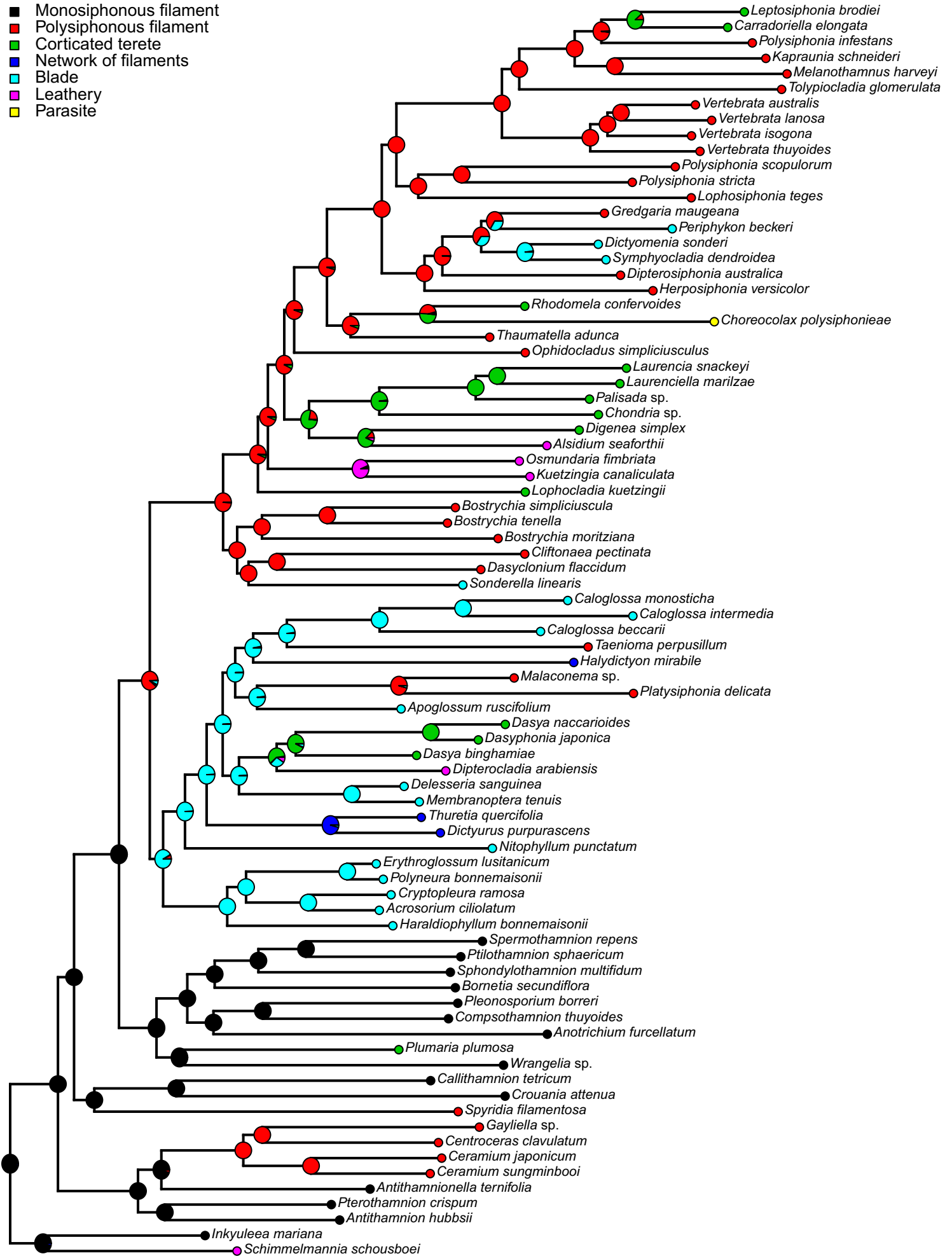
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- Monosiphonous filament
- Polysiphonous filament
- Corticated terete
- Network of filaments
- Blade
- Leathery
- Parasite



Supplemental data 1. Glossary. Extracted from Maggs & Hommersand, 1993, with permission.

**Auxiliary cell** Cell that receives the diploid nucleus from the carpogonium and gives rise to the gonimoblast (Fig. S2B).

**Carpogonial branch** Filament bearing the female gametangium, the carpogonium (Fig. S2A).

**Carpogonium** Female gametangium (Fig. S2A).

**Corticated** With a secondary cortex formed by development of filaments within, and sometimes outside, the outer walls of primary filaments (Figs 1H-K).

**Cystocarp** The gonimoblast tissue and surrounding gametophytic pericarp tissue; structure from which carpospores are released (Fig. S2C).

**Gonimoblast** Tissue which develops on the female plant after fertilization and which ultimately produces carposporangia (Fig. S2C).

**Gonimoblast initial** The first cell arising from a fertilized carpogonium or diploidized auxiliary cell, which develops into the gonimoblast.

**Monopodial** Development in which the primary axis is maintained as the main line of growth and other axes are produced from it (Fig. S1A in supplementary material).

**Monosiphonous** Consisting of a single row of cells, with or without cortication but without periaxial cells (cf. polysiphonous) (Fig. 1A).

**Periaxial (= pericentral) cell** One of a number, often a ring, of cells cut off from and surrounding an axial cell.

**Pericarp** That part of the cystocarp produced by the female gametangial thallus and forming a covering to the developing gonimoblast (Fig. S2C).

**Polysiphonous** With each axial cell surrounded, usually over its entire length, with a particular number of periaxial cells (Figs 1B-E).

**Supporting cell** Cell bearing one or more carpogonial branches (Fig. S2A).

**Sympodial** Development in which the primary axis is continually being replaced by lateral axes which become temporarily dominant, but soon are replaced by their own laterals (Fig. S1B).

**Uniaxial** Containing only a single axial filament.

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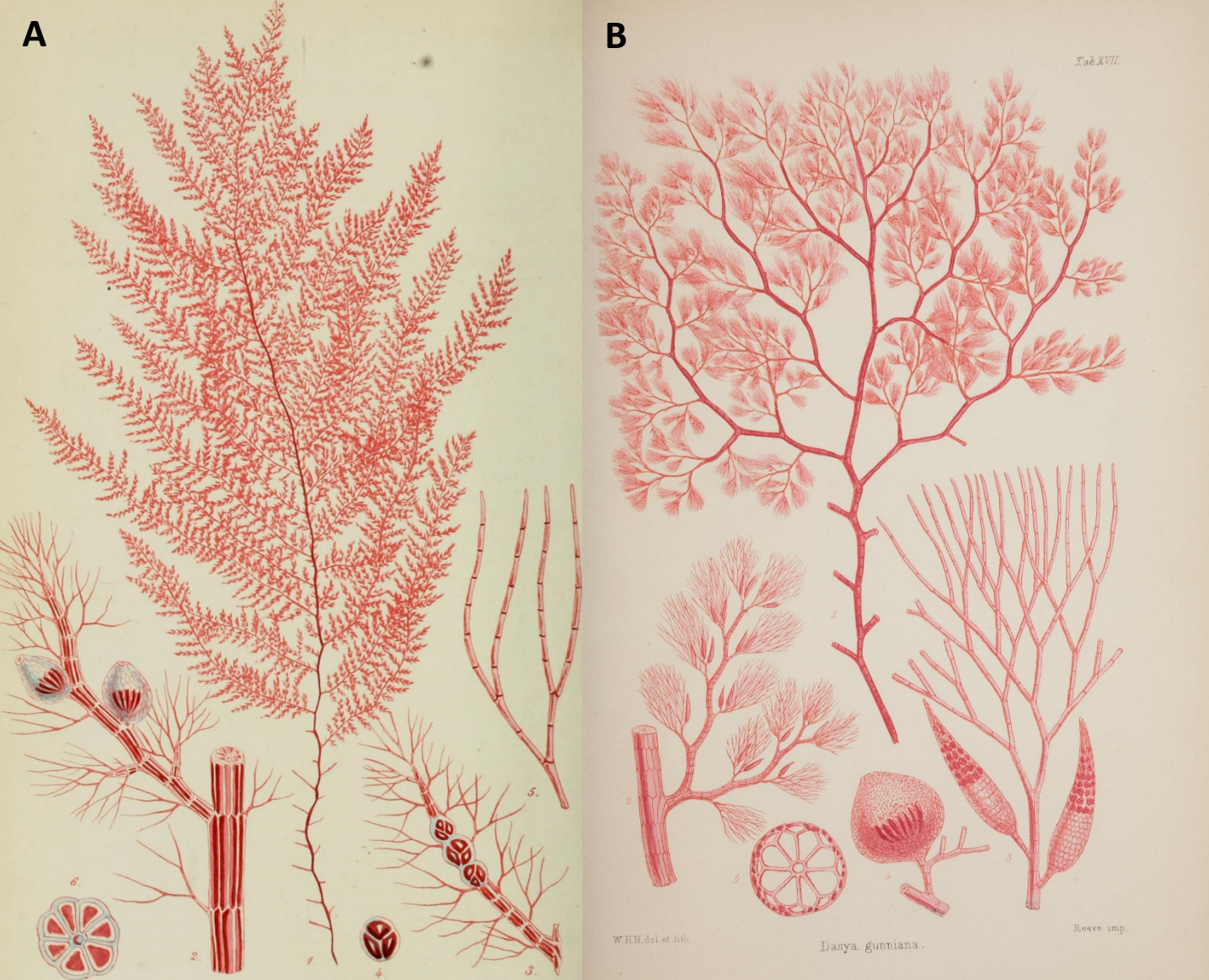


Fig. S1. (A) *Vertebrata byssoides*, thallus with monopodial growth. (B) *Dasya gunniana*, thallus with sympodial growth. Images taken from Harvey (1847, 1850).

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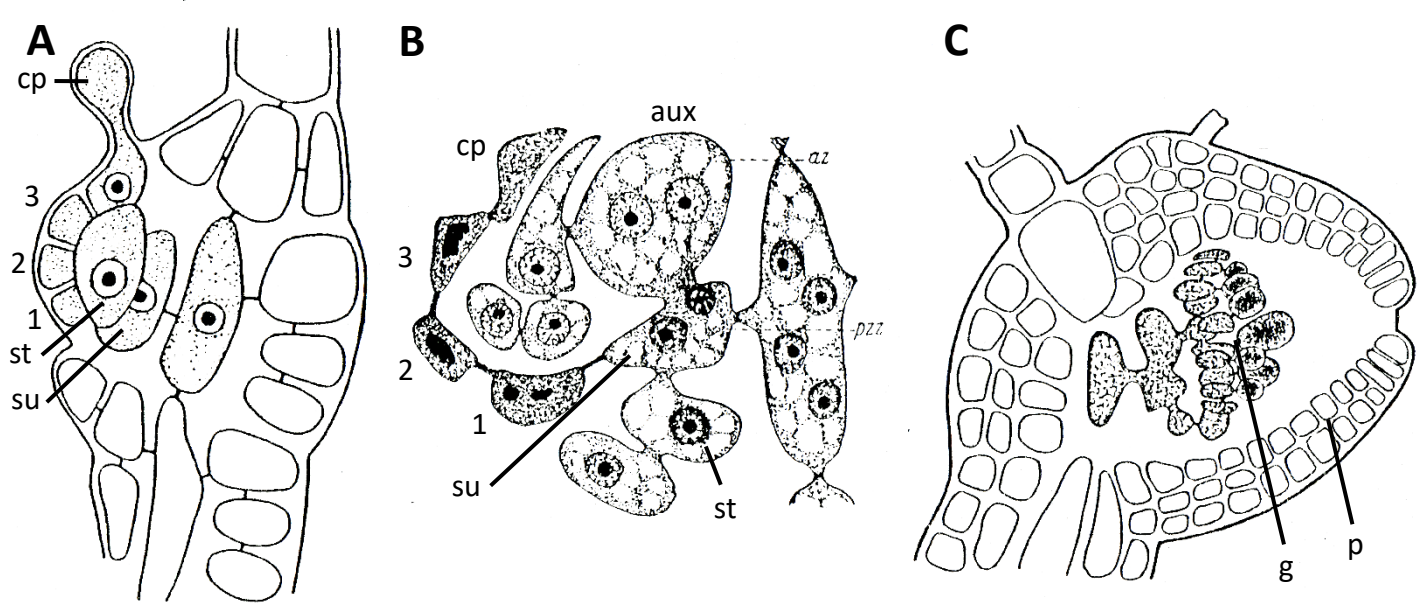
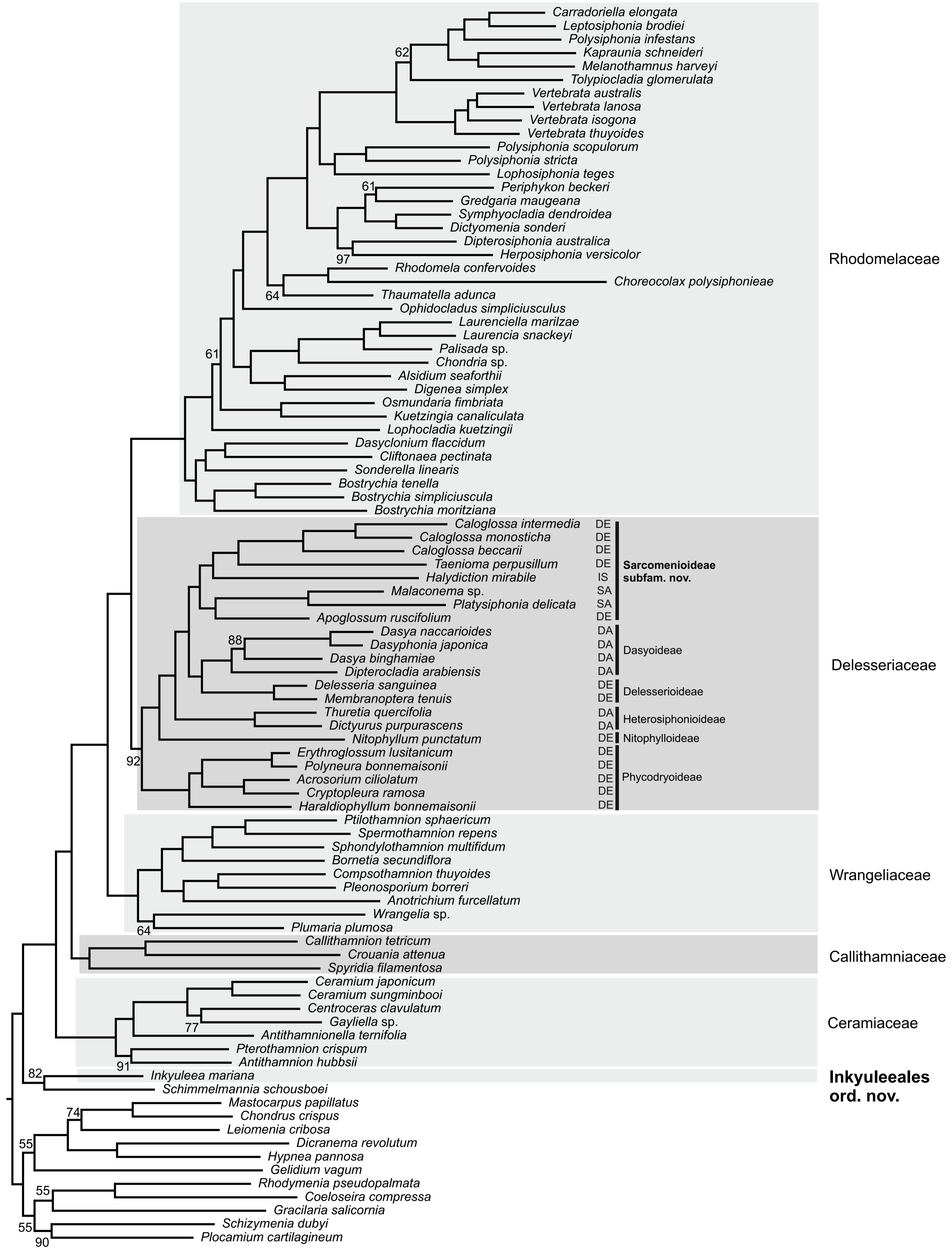


Fig. S2. *Rhodomela virgata*. Procarp and gonimoblast development. (A) Procarp consisting on a supporting cell (su), a sterile cell (st), and a carpoogonial branch (1-3) bearing the carpoogonium (cp). (B) After the fertilization, the supporting cell (su) produces an auxiliary cell (aux). (C) Cystocarp consisting on the gonimoblast (g) resulting from the divisions of the auxiliary cell that is surrounded by the pericarp (p). Images taken from Kylin 1956.

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- Monosiphonous filament
- Polysiphonous filament
- Corticated terete
- Network of filaments
- Blade
- Leathery
- Parasite

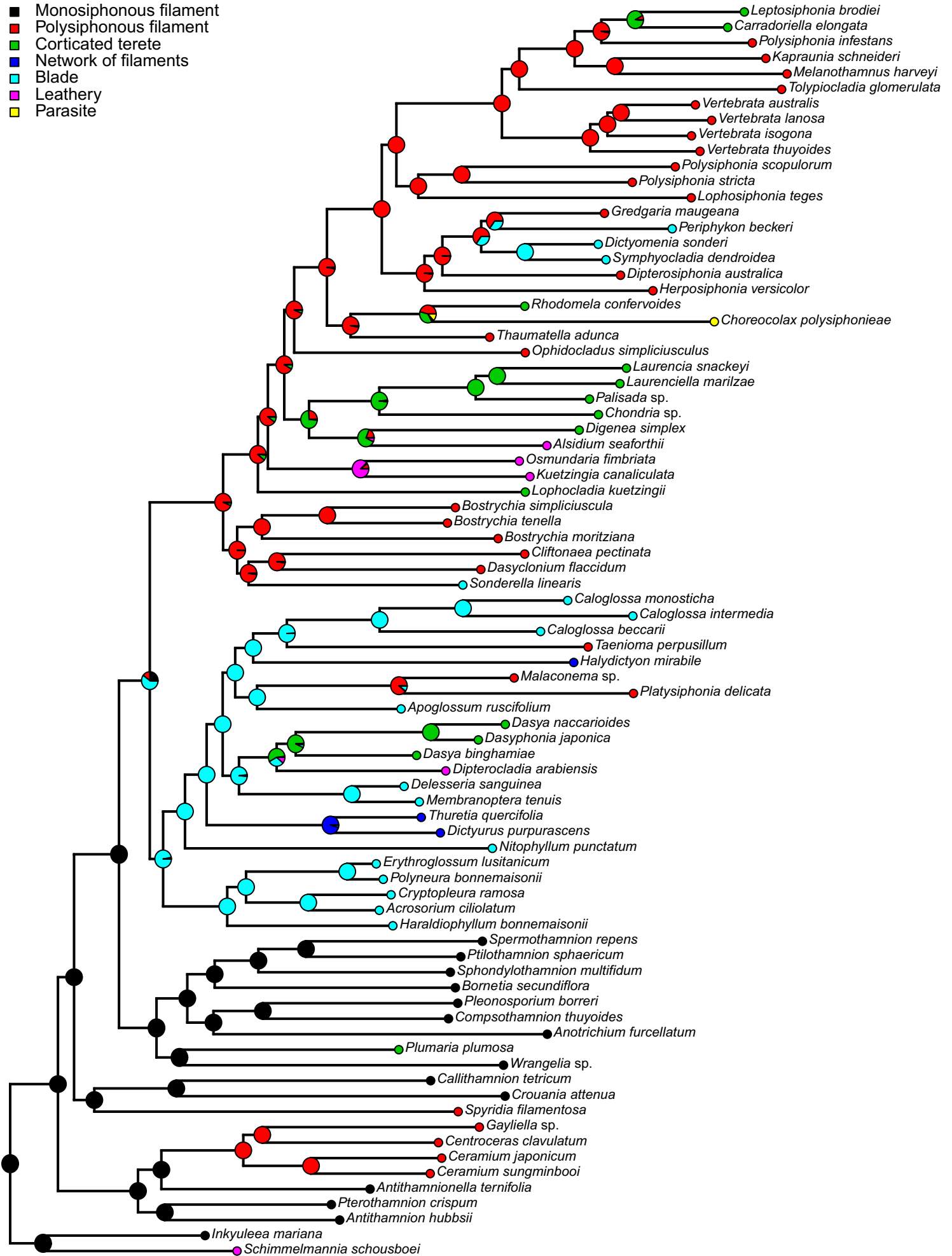


Table S1. Classification of genera and tribes of the Ceramiales mainly based in works including molecular data (excluding the Rhodomelaceae, see Díaz-Tapia et al. 2017).

Choi et al. (2001)	Lin et al. (2001)	Choi et al. (2002)	Genera and tribes proposed after Lin et al. 2001, Choi et al. 2001, 2002	This work
<b>CERAMIALES</b>				<b>INKYULEEAELES</b>
<b>Inkyuleeaceae</b>				<b>Inkyuleeaceae</b>
<i>Inkyuleea</i>				<i>Inkyuleea</i>
<b>Ceramiaceae</b>			<b>Ceramiaceae</b>	<b>CERAMIALES</b>
Antithamnieae				<b>Ceramiaceae</b>
<i>Antithamnion</i>				Antithamnieae
Ceramiaceae				<i>Antithamnion</i>
				Ceramiaceae
<i>Carpoblepharis</i>			<sup>1</sup> <i>Campylaephora</i>	
<i>Centroceras</i>				<i>Centroceras</i>
<i>Ceramium</i>				<i>Ceramium</i>
			<sup>2</sup> <i>Corallophila</i>	
			<sup>2</sup> <i>Gayliella</i>	<i>Gayliella</i>
			<sup>2</sup> <i>Herpochondria</i>	
			<sup>2</sup> <i>Microcladia</i>	
			<sup>2</sup> <i>Reinboldiella</i>	
Dohrnielleae				Dohrnielleae
<i>Antithamnionella</i>				<i>Antithamnionella</i>
Heterothamnieae				
<i>Heterothamnion</i>				
Pterothamnieae				Pterothamnieae
<i>Pterothamnion</i>				<i>Pterothamnion</i>
<i>Incertae sedis</i>				
<i>Tetrathamnion</i>				
<b>Callithamniaceae</b>			<b>Callithamniaceae</b>	<b>Callithamniaceae</b>
Callithamnieae				Callithamnieae
<i>Aglaothamnion</i>				
<i>Callithamnion</i>			<sup>3</sup> <i>Aristoptilon</i>	<i>Callithamnion</i>
<i>Diapse</i>			<sup>3</sup> <i>Carpothamnion</i>	
			<sup>3</sup> <i>Falklandiella</i>	
			<sup>3</sup> <i>Georgiella</i>	
Crouanieae				Crouanieae
<i>Crouania</i>				<i>Crouania</i>
			<sup>4</sup> <i>Gulsonia</i>	
			<sup>3</sup> <i>Heteroptilon</i>	
			<sup>3</sup> <i>Ptilocladia</i>	
Euptiloteae				
<i>Euptilota</i>				
<i>Seirospora</i>				
			<sup>3</sup> <i>Sciurothamnion</i>	
Rhodocallideae				

Choi et al. (2001)  
**Spyridiaceae**

Lin et al. (2001)

Choi et al. (2002)

*Spyridia*

Spyridieae  
*Spyridia*

**Wrangeliaceae**

**Wrangeliaceae**

**Wrangeliaceae**

Compsothamnieae  
*Compsothamnion*  
*Dasythamnionella*

Compsothamnieae  
*Compsothamnion*

Dasyphileae  
*Dasyphila*  
*Muellerena*

Griffithsieae  
*Anotrichium*

Griffithsieae  
*Anotrichium*  
*Bornetia*

*Griffithsia*  
*Halurus*

Monosporeae  
*Monosporus*

Ptiloteae  
*Neoptilota*  
*Plumaria*  
*Ptilota*

Ptiloteae  
*Plumaria*

Spermothamnieae  
*Lejolisia*

Spermothamnieae  
<sup>5</sup>*Ptilothamnion*  
*Spermothamnion*

*Spermothamnion*  
Sphondylothamnieae  
*Involucrana*  
*Shepleya*

Sphondylothamnieae  
*Sphondylothamnion*

Spongoclonieae  
*Pleonosporium*  
*Spongoclonium*

Spongoclonieae  
*Pleonosporium*

Wrangelieae  
*Wrangelia*

Wrangelieae  
*Wrangelia*

***Incertae sedis***

*Warrenia*



Choi et al. (2001)	Lin et al. (2001)	Choi et al. (2002)	Genera and tribes proposed after Lin et al. 2001, Choi et al. 2001, 2002	This work
	<b>Delesseriaceae</b>		<b>Delesseriaceae</b>	<b>Delesseriaceae</b>
	<b>Delesserioideae</b>		<b>Delesserioideae</b>	<b>Sarcomenioideae</b>
	Sarcomenieae			subfam. nov.
	<i>Sarcomenia</i>			Sarcomenieae
				<i>Malaconema</i>
				<i>Platysiphonia</i>
	Caloglosseae			Caloglosseae
	<i>Caloglossa</i>			<i>Caloglossa</i>
				<i>Taenioma</i>
	Apoglosseae			Apoglosseae
	<i>Apoglossum</i>			<i>Apoglossum</i>
	<i>Paraglossum</i>			
	<i>Claudea</i> group		<sup>6</sup> <i>Phrix</i>	
	<i>Vanvoorstia</i>		<sup>7</sup> Claudeeae	
				Halydictyeae trib. nov.
				<i>Halydictyon</i>
				<b>Delesserioideae</b>
	Hemineureae		<sup>8</sup> Botryocarpeae	
	<i>Botryocarpa</i>			
	<i>Hemineura</i>			
	<i>Laingia</i>			
	<i>Marionella</i>			
	<i>Patulophycus</i>			
	<i>Pseudophycodrys</i>			
	Hypoglosseae			
	<i>Hypoglossum</i>			
	<i>Zellera</i>			
	<i>Bartoniella</i>			
	<i>Branchioglossum</i>			
	Delesserieae			Delesserieae
	<i>Delesseria</i>			<i>Delesseria</i>
			<sup>8</sup> Membranopterae	Membranopterae
	<i>Membranoptera</i>			<i>Membranoptera</i>
	Grinnellieae			
	<i>Grinnellia</i>		<sup>9</sup> Wynneophycuseae	
			<sup>9</sup> <i>Wynneophycus</i>	

Choi et al. (2001)	Lin et al. (2001)	Choi et al. (2002)	Genera and tribes proposed after Lin et al. 2001, Choi et al. 2001, 2002	This work
	<b>Phycodryoideae</b>		<b>Phycodryoideae</b>	<b>Phycodryoideae</b>
	Phycodryeae			Phycodryeae
	<i>Cladodonta</i>			<i>Erythroglossum</i>
	<i>Heterodoxia</i>		<sup>10</sup> <i>Hymenenopsis</i>	
	<i>Nienburgia</i>			
	<i>Phycodrys</i>			
	<i>Polyneura</i>			<i>Polyneura</i>
	<i>Womersleya</i>			
	Myriogrammeae			Myriogrammeae
	<i>Myriogramme</i>		<sup>11</sup> <i>Neoharaldiophyllum</i>	
	<i>Haraldiophyllum</i>			<i>Haraldiophyllum</i>
	Schizoserideae			
	<i>Abroteia</i>			
	<i>Drachiella</i>			
	<i>Neuroglossum</i>			
	<i>Schizoseris</i>			
	Cryptopleureae			Cryptopleureae
	<i>Acrosorium</i>			<i>Acrosorium</i>
	<i>Cryptopleura</i>			<i>Cryptopleura</i>
	<i>Hymenena</i>			
	<i>Botryoglossum</i>			
	<b>Nitophylloideae</b>		<b>Nitophylloideae</b>	<b>Nitophylloideae</b>
	Nitophylleae			Nitophylleae
	<i>Nitophyllum</i>		<sup>12</sup> <i>Augophyllum</i>	<i>Nitophyllum</i>
	<i>Calonitophyllum</i>		<sup>8</sup> Valeriemayeeae	
	<i>Polyneuropsis</i>			
	<i>Valeriemaya</i>			
	Martensieae			
	<i>Martensia</i>			
	<i>Opephyllum</i>			
		<b>Dasyaceae</b>		
		<b>Heterosiphonoideae</b>		<b>Heterosiphonoideae</b>
		<i>Dictyurus</i>		<i>Dictyurus</i>
		<i>Heterosiphonia</i>		
		<i>Thuretia</i>		<i>Thuretia</i>
		<b>Dasyoideae</b>		<b>Dasyoideae</b>
		<i>Dasya</i>		<i>Dasya</i>
		<i>Dasyphonia</i>		<i>Dasyphonia</i>
		<i>Eupogodon</i>		<i>Dipterocladia</i>
		<i>Rhodoptilum</i>		

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Table S2. GenBank accession numbers of the chloroplast genomes included in the phylogenetic analysis.

Species	Collection site; date; habitat; collectors / Publication	ID	Genbank accession number	Length when incomplete/number of CDSs
<i>Acrosorium ciliolatum</i>	Díaz-Tapia et al. 2017	-	MF101411	
<i>Alsidium seaforthii</i>	Díaz-Tapia et al. 2017, as <i>Bryothamnion</i>	PD644	MF101430	
<i>Anotrichium furcellatum</i>	Perbes, A Coruña, Spain; 15.i.2017; intertidal; PD	PD2933	XXXX	170.239 / 192
<i>Antithamnion habsii</i>	Baiona, Pontevedra, Spain; 3.v.2016; pontoon in a marina; PD	PD2206	XXXX	152.684 / 175
<i>Antithamnionella ternifolia</i>	Dique Abrigo, A Coruña, Spain; 12.iii.2017; pontoon in a marina; PD	PD2956	XXXX	
<i>Apoglossum ruscifolium</i>	Perbes, A Coruña, Spain; 15.i.2017; intertidal; PD	PD2929	XXXX XXXX XXXX XXXX	30.775 / 31 30.076 / 35 21.752 / 25 84,340 / 97
<i>Bornetia secundiflora</i>	Perbes, A Coruña, Spain; 15.i.2017; intertidal; PD	PD2926	XXXX	
<i>Bostrychia moritziana</i>	Díaz-Tapia et al. 2017	JW3660	MF101419	
<i>Bostrychia simpliciuscula</i>	Díaz-Tapia et al. 2017	JW3897	MF101421	
<i>Bostrychia tenella</i>	Díaz-Tapia et al. 2017	JW3079	MF101417	
<i>Callithamnion tetricum</i>	Perbes, A Coruña, Spain; 15.i.2017; intertidal; PD	PD2927	XXXX	166.571 / 188
<i>Caloglossa beccarii</i>	Díaz-Tapia et al. 2017	JW4523	MF101422	
<i>Caloglossa intermedia</i>	Díaz-Tapia et al. 2017	JW3535	MF101418	
<i>Caloglossa monosticha</i>	Díaz-Tapia et al. 2017	JW3046	MF101416	
<i>Carradoriella elongata</i>	Díaz-Tapia et al. 2017, as <i>Polysiphonia</i>	PD547	MF101427	
<i>Centroceras clavulatum</i>	Swan Bay, Victoria, Australia; 23.xi.2017; intertidal; HV	HV06547	XXXX XXXX XXXX	30.045 / 38 53.556 / 63 76.977 / 89
<i>Ceramium japonicum</i>	Lee et al. 2016a	-	KX284719	
<i>Ceramium sungminbooi</i>	Hughey & Boo 2016	UC2050592	NC031211	
<i>Chondria</i> sp.	Díaz-Tapia et al. 2017	PD1582	MF101451	
<i>Choreocolax polysiphoniae</i>	Salomaki et al. 2015	-	KP308096	

<i>Cliftonaea pectinata</i> <i>Compsothamnion thuyoides</i>	Díaz-Tapia et al. 2017	PD1561	MF101450	
	Margaritas, A Coruña, Spain; 16.i.2017; intertidal; PD	PD2939	XXXX	10.141 / 4
			XXXX	2.626 / 3
			XXXX	3.765 / 5
			XXXX	8.533 / 6
			XXXX	6.559 / 9
			XXXX	1.501 / 1
			XXXX	6.831 / 8
			XXXX	9.408 / 4
			XXXX	3.795 / 5
			XXXX	5.858 / 6
			XXXX	26.665 / 46
			XXXX	4.324 / 6
<i>Crouania attenuata</i> <i>Cryptopleura ramosa</i>	San Pedro, A Coruña, Spain; 17.i.2017; intertidal; PD	PD2952	XXXX	
	Perbes, A Coruña, Spain; 15.i.2017; intertidal; PD	PD2928	XXXX	10.593 / 4
			XXXX	8.392 / 11
			XXXX	33.660 / 38
			XXXX	4.623 / 5
			XXXX	11.942 / 14
			XXXX	79.318 / 91
			XXXX	14.233 / 20
<i>Dasya binghamiae</i> <i>Dasya naccarioides</i>	Tamayo & Hughey 2016	UC2050572	KX247284	
	Díaz-Tapia et al. 2017	PD888	MF101436	
<i>Dasyclonium flaccidum</i>	Díaz-Tapia et al. 2017	PD1087	MF101443	
<i>Dasyphonia japonica</i>	Margaritas, A Coruña, Spain; 16.i.2017; boat rope; PD	PD2948	XXXX	15.673 / 13
			XXXX	50.132 / 60
			XXXX	44.819 / 44
			XXXX	32.671 / 54
			XXXX	7.348 / 10
			XXXX	8.472 / 11
			XXXX	5.683 / 7

<i>Delesseria sanguinea</i>	Ringstead Bay, Dorset, UK; 13.iv.2017; drift; CAM	PD3001	XXXX	21.358 / 24
			XXXX	15.106 / 20
			XXXX	77.308 / 91
			XXXX	15.713 / 19
<i>Dictyomenia sonderi</i>	Díaz-Tapia et al. 2017	PD1725	MF101455	
<i>Dictyurus purpurascens</i>	Matemwe, Zanzibar, Tanzania; 9.ii.2008; reef crest	TZ0704	XXXX	
<i>Digenea simplex</i>	Díaz-Tapia et al. 2017	PD1820	MF101465	
<i>Dipterocladia arabiensis</i>	Díaz-Tapia et al. 2017	DHO101	MF101408	
<i>Dipterosiphonia australica</i>	Díaz-Tapia et al. 2017	PD1107	MF101444	
<i>Erythroglossum lusitanicum</i>	Margaritas, A Coruña, Spain; 16.i.2017; intertidal; PD	PD2950	XXXX	38.724 / 43
			XXXX	22.505 / 21
			XXXX	20.537 / 17
			XXXX	16.556 / 19
			XXXX	20.200 / 24
			XXXX	37.047 / 51
<i>Gayliella</i> sp.	Coral Bay, Western Australia; v.2013; epiphyte on <i>Laurencia snackeyi</i> ; JFC	JFC0032b	XXXX	147.392 / 175
<i>Gredgaria maugeana</i>	Díaz-Tapia et al. 2017	PD1230	MF101446	
<i>Halydictyon mirabile</i>	Sausset les Pins, Marseilles, France; 11.v.2011; IB & MV	SANT-25966	XXXX	15.821 / 18
			XXXX	5.207 / 7
			XXXX	8.365 / 15
			XXXX	10.717 / 9
			XXXX	17.718 / 14
			XXXX	14.680 / 17
			XXXX	10.749 / 14
			XXXX	17.640 / 32
			XXXX	12.589 / 12
XXXX	7.895 / 11			

<i>Haraldiophyllum bonnemaisonii</i>	Morás, Lugo, Spain; 15.xi.2004; intertidal; IB	S15261	XXXX	10.293 / 4																					
			XXXX	5.280 / 7																					
			XXXX	3.667 / 5																					
			XXXX	15.595 / 12																					
			XXXX	4.494 / 6																					
			XXXX	17.690 / 13																					
			XXXX	20.256 / 23																					
			XXXX	24.021 / 37																					
			XXXX	6.993 / 8																					
<i>Herposiphonia versicolor</i>	Díaz-Tapia et al. 2017	PD852	MF101434																						
			<i>Kapraunia schneideri</i>	Díaz-Tapia et al. 2017, as <i>Polysiphonia</i>	PD1720	MF101454																			
						<i>Kuetzingia canaliculata</i>	Díaz-Tapia et al. 2017	PD1540	MF101449																
									<i>Laurencia snackeyi</i>	Verbruggen & Costa 2015	JFC0032	LN833431													
												<i>Laurenciella marilzae</i>	Díaz-Tapia et al. 2017	H.1501	MF101410										
															<i>Leptosiphonia brodiei</i>	Díaz-Tapia et al. 2017, as <i>Polysiphonia</i>	PD516	MF101425							
																		<i>Lophocladia kuetzingii</i>	Díaz-Tapia et al. 2017	PD1509	MF101448				
																					<i>Lophosiphonia teges</i>	Díaz-Tapia et al. 2017	PD1823	MF101457-64	
																								MF101466	
<i>Malaconema</i> sp.	Queenscliff, Victoria, Australia; 03.xii.2016; drift; PD	PD2901																						XXXX	6.754 / 1
			XXXX	1.327 / 2																					
			XXXX	1.249 / 1																					
			XXXX	1.874 / 2																					
			XXXX	5.017 / 2																					
			XXXX	4.120 / 5																					
			XXXX	2.438 / 4																					
			XXXX	9.146 / 3																					
			XXXX	3.639 / 5																					
XXXX	5.899 / 5																								
XXXX	1.657 / 3																								
XXXX	3.470 / 6																								

			XXXX	5.886 / 10
			XXXX	2.016 / 3
			XXXX	4.043 / 4
			XXXX	3.016 / 5
			XXXX	2.524 / 2
<i>Melanothamnus harveyi</i>	Díaz-Tapia et al. 2017	PD890	MF101437	
<i>Membranoptera tenuis</i>	Hughey et al. 2017	UC266439	KP675983	
<i>Nitophyllum punctatum</i>	Perbes, A Coruña, Spain; 15.i.2017; intertidal; PD	PD2930	XXXX	
<i>Ophidocladus simpliciusculus</i>	Díaz-Tapia et al. 2017	PD949	MF101440	
<i>Osmundaria fimbriata</i>	Díaz-Tapia et al. 2017	JW2841	MF101415	
<i>Palisada</i> sp.	Díaz-Tapia et al. 2017	PD1686	MF101453	
<i>Periphykon beckeri</i>	Díaz-Tapia et al. 2017	JH1427	MF101413	
<i>Platysiphonia delicata</i>	Díaz-Tapia et al. 2017	H.1445	MF101409	
<i>Pleonosporium borreri</i>	Margaritas, A Coruña, Spain; 16.i.2017; intertidal; PD	PD2941	XXXX	36.943 / 38
			XXXX	54.389 / 62
			XXXX	77.716 / 90
<i>Plumaria plumosa</i>	As Amorosas, A Coruña, Spain; 19.i.2017; intertidal; PD	PD2953	XXXX	7.535 / 2
			XXXX	5.898 / 6
			XXXX	2.520 / 3
			XXXX	21.584 / 22
			XXXX	79.630 / 91
			XXXX	4.307 / 6
			XXXX	10.675 / 10
<i>Polysiphonia infestans</i>	Díaz-Tapia et al. 2017	PD763	MF101432	
<i>Polysiphonia scopulorum</i>	Díaz-Tapia et al. 2017	PD899	MF101438	
<i>Polysiphonia stricta</i>	Díaz-Tapia et al. 2017	PD550	MF101428	
<i>Polyneura bonnemaisonii</i>	Mudeford, Dorset, UK; 16.iv.2017; drift; CAM	PD2997	XXXX	10.135 / 4
			XXXX	4.926 / 7
			XXXX	6.353 / 10
			XXXX	16.135 / 15
			XXXX	18.051 / 14



			XXXX	6.714 / 6
			XXXX	10.112 / 10
			XXXX	17.021 / 21
			XXXX	2.973 / 5
<i>Pterothamnion crispum</i>	San Ciprián, Xove, Lugo, Spain; 21.vii.2015; subtidal (5 m); IB	SANT-29588	XXXX	7.605 / 11
			XXXX	20.685 / 21
			XXXX	4.837 / 7
			XXXX	27.993 / 23
			XXXX	30.660 / 45
			XXXX	15.472 / 19
			XXXX	2.583 / 2
			XXXX	3.075 / 1
<i>Ptilothamnion sphaericum</i>	Margaritas, A Coruña, Spain; 16.i.2017; intertidal; PD	PD2949	XXXX	5.109 / 8
			XXXX	11.026 / 14
			XXXX	30.626 / 36
			XXXX	20.726 / 17
			XXXX	14.322 / 15
			XXXX	9.144 / 9
			XXXX	30.672 / 44
			XXXX	3.156 / 5
<i>Rhodomela confervoides</i>	Díaz-Tapia et al. 2017	PD508	MF101424	
<i>Sonderella linearis</i>	Díaz-Tapia et al. 2017	PD1151	MF101445	
<i>Spermothamnion repens</i>	Margaritas, A Coruña, Spain; 16.i.2017; intertidal; PD	PD2951	XXXX	
<i>Sphondylothamnion multifidum</i>	Punta Insua, Carnota, A Coruña, Spain; 21.iv.2017; subtidal (2 m); IB	PD2995	XXXX	170.380 / 194
<i>Spyridia filamentosa</i>	Díaz-Tapia et al. 2017	PD1020	MF101441	
<i>Symphycladia dendroidea</i>	Díaz-Tapia et al. 2017	JW3780	MF101420	
<i>Taenioma perpusillum</i>	Díaz-Tapia et al. 2017	PD1676	MF101452	
<i>Thaumatella adunca</i>	Díaz-Tapia et al. 2017	PD1388	MF101447	
<i>Thuretia quercifolia</i>	Díaz-Tapia et al. 2017	PD1024	MF101442	

<i>Tolypocladia glomerulata</i>	Díaz-Tapia et al. 2017	PD1825	MF101467	
<i>Vertebrata australis</i>	Díaz-Tapia et al. 2017	PD931	MF101439	
<i>Vertebrata isogona</i>	Díaz-Tapia et al. 2017	PD831	MF101433	
<i>Vertebrata lanosa</i>	Salomaki et al. 2015	-	KP308097	
<i>Vertebrata thuyoides</i>	Díaz-Tapia et al. 2017	PD546	MF101426	
<i>Wrangelia</i> sp.	Pebbly beach, Victoria, Australia; 9.xi.2016; intertidal; PD, HV & KD	PD2766	XXXX	10.291 / 5
			XXXX	8.502 / 12
			XXXX	19.311 / 18
			XXXX	10.967 / 13
			XXXX	35.573 / 33
			XXXX	40.772 / 56
<b>OUTGROUP</b>				
<i>Chondrus crispus</i>	Collén et al. 2013	PCG	NC020795	
<i>Coeloseira compressa</i>	Kilpatrick & Hughey 2015	UC2050599	KU053957	
<i>Dicranema revolutum</i>	Australia, Victoria, Pt Lonsdale; 8.xi.2014; epiphyte of <i>Amphibolis antarctica</i> ; VRM	VRM0320	XXXX	
<i>Gelidium vagum</i>	Lee et al. 2016b	-	NC029859	
<i>Gracilaria salicornia</i>	Campbell et al. 2014	ARS08332	NC023785	
<i>Hypnea pannosa</i>	Australia, Queensland, Heron Island; 14.v.2015; reef flat	HV5551	XXXX	
<i>Inkyuleea mariana</i>	Merry Island, Victoria, Australia; 29.xii.2014; drift; PD	PD1141	XXXX	
<i>Leiomenia cribosa</i>	Australia, Victoria, Queenscliff, Popes Eye; 8.xii.2014; subtidal reef	HV05337	XXXX	
<i>Mastocarpus papillatus</i>	Sissini et al. 2016	UC2050562	KX525588	
<i>Plocamium cartilagineum</i>	Lee et al. 2016a	-	KX284727	
<i>Rhodomenia pseudopalmata</i>	Lee et al. 2016a	-	KX284709	
<i>Schimmelmanna schousboei</i>	Lee et al. 2016a	-	KX284711	
<i>Schizymenia dubyi</i>	Lee et al. 2016a	-	KX284712	

Collectors: PD = Pilar Díaz-Tapia; HV = Heroen Verbruggen; CAM = Christine A. Maggs; KD = Kyatt Dixon; IB = Ignacio Bárbara; JFC = Joana F. Costa; MV = Marc Verlaque; VRM = Vanessa R. Marcelino.

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