



**The genera *Melanothamnus* Bornet & Falkenberg and *Vertebrata* S.F. Gray constitute well-defined clades of the red algal tribe Polysiphonieae (Rhodomelaceae, Ceramiales)**

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9 2 **defined clades of the red algal tribe Polysiphonieae (Rhodomelaceae, Ceramiales)**

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24 ABSTRACT

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26 *Polysiphonia* is the largest genus of red algae, and several schemes subdividing it into smaller taxa

27 have been proposed since its original description. Most of these proposals were not generally

28 accepted, and currently the tribe Polysiphonieae consists of the large genus *Polysiphonia* (190

29 species), the segregate genus *Neosiphonia* (43 species), and 13 smaller genera (< 10 species each).

30 In this paper, phylogenetic relationships of the tribe Polysiphonieae are analysed, with particular

31 emphasis on the genera *Carradoriella*, *Fernandosiphonia*, *Melanothamnus*, *Neosiphonia*,

32 *Polysiphonia sensu stricto*, *Streblocladia* and *Vertebrata*. We evaluated the consistency of 14

33 selected morphological characters in the identified clades. Based on molecular phylogenetic (*rbcL*

34 and 18S genes) and morphological evidence, two speciose genera are recognized: *Vertebrata*

35 (including the type species of the genera *Ctenosiphonia*, *Enelittosiphonia*, *Boergeseniella* and

36 *Brongniartella*) and *Melanothamnus* (including the type species of the genera *Fernandosiphonia*

37 and *Neosiphonia*). Both genera are distinguished from other members of the Polysiphonieae by

38 synapomorphic characters, the emergence of which could have provided evolutionarily selective

39 advantages for these two lineages. In *Vertebrata* trichoblast cells are multinucleate, possibly

40 associated with the development of extraordinarily long, photoprotective, trichoblasts.

41 *Melanothamnus* has 3-celled carpogonial branches and plastids lying exclusively on radial walls of

42 the pericentral cells, which similarly may improve resistance to damage caused by excessive light.

43 Other relevant characters that are constant in each genus are also shared with other clades. The

44 evolutionary origin of the genera *Melanothamnus* and *Vertebrata* is estimated as 75.7-95.78 and

45 90.7-138.66 Ma, respectively. Despite arising in the Cretaceous, before the closure of the Tethys

46 Seaway, *Melanothamnus* is a predominantly Indo-Pacific genus and its near-absence from the

47 northeastern Atlantic is enigmatic. The nomenclatural implications of this work are that 46 species

48 are here transferred to *Melanothamnus*, six species are transferred to *Vertebrata* and 13 names are

49 resurrected for *Vertebrata*.

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52 **Key words:** biogeography, evolution, molecular systematics, morphology, phylogeny,

53 *Polysiphonia*, red algae, time calibration

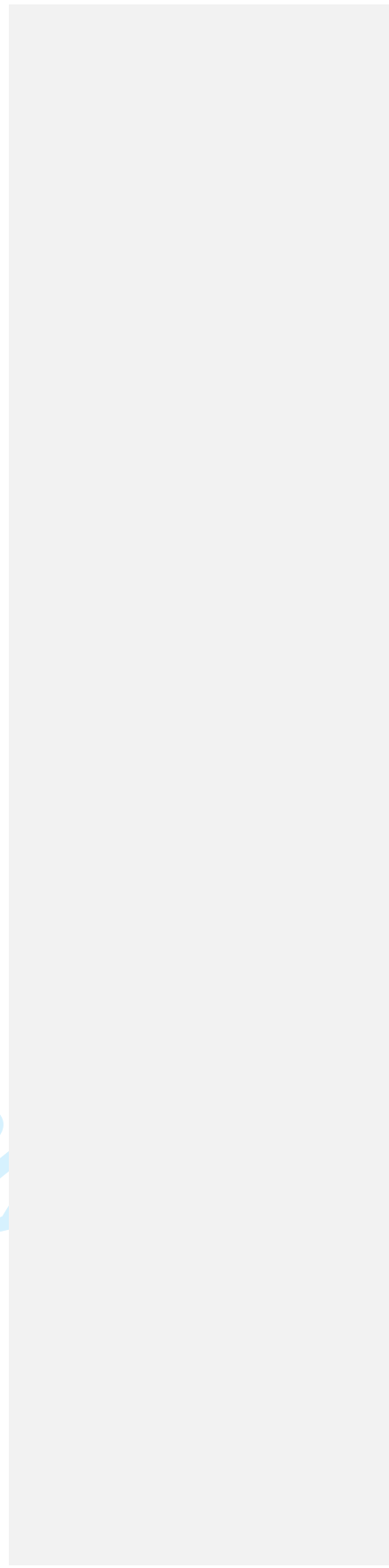
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## 58 INTRODUCTION

59 The Rhodomelaceae Areschoug is the largest family of red algae, currently including more than  
60 1,000 species (Guiry & Guiry, 2016). It consists of the tribes Amansieae [Schmitz \(1889\)](#),  
61 Bostrychieae [Falkenberg \(1901\)](#), Chondriaceae [Schmitz & Falkenberg \(1897\)](#), Herposiphoniae  
62 [Schmitz & Falkenberg \(1897\)](#), Heterocladieae [Falkenberg \(1901\)](#), Laurencieae [Schmitz \(1889\)](#),  
63 Lophothalieae [Schmitz & Falkenberg \(1897\)](#), Neotenophyceae [Kraft & I.A.Abbott \(2002\)](#),  
64 Pleurostichidiaceae ([Hommersand, 1963](#)), Polysiphoniae [Schmitz \(1889\)](#), Polyzoniae [Schmitz &](#)  
65 [Falkenberg \(1897\)](#), Pterosiphoniae [Falkenberg \(1901\)](#), Rhodomeleae [Schmitz & Falkenberg](#)  
66 [\(1897\)](#), Sonderelleae [L.E.Phillips \(2001\)](#) and Streblocladiaceae nom. nud. ([Hommersand, 1963](#);  
67 [Kraft & Abbott, 2002](#); [Womersley, 2003](#)), of which the most speciose is the Polysiphoniae with  
68 over 300 species in 15 currently recognized genera (Guiry & Guiry, 2016).

69 Within the Polysiphoniae the genus *Polysiphonia* Greville (1824), nom. cons., has  
70 representatives throughout the world, in the majority of photic marine benthic habitats including  
71 brackish ones (e.g. [Womersley, 1979](#); [Hollenberg, 1942, 1944, 1968a, 1968b](#); [Maggs &](#)  
72 [Hommersand, 1993](#); [Lam et al., 2013](#)). *Polysiphonia* is poorly circumscribed, and has remained in  
73 a state of taxonomic flux since its original description. Numerous schemes for subdividing this  
74 large and morphologically diverse genus into smaller and more manageable groups have been  
75 proposed (e.g. [Segi, 1951](#); [Hollenberg, 1968a, 1968b](#)), based mostly on the number of periaxial  
76 cells, either four (subgenus *Oligosiphonia*) or more than four (subgenus *Polysiphonia*). These  
77 schemes have generally been rejected and several generic names [e.g. *Orcasia* [Kylin \(1941\)](#), based  
78 on *Polysiphonia senticulosa* [Harvey](#)] are currently regarded as synonyms of *Polysiphonia*.  
79 However, despite having been subsumed within *Polysiphonia* in most classification schemes,  
80 *Vertebrata* [S.F.Gray \(1821\)](#) is currently recognized as a monospecific genus containing only the  
81 type species, *V. lanosa* ([Linnaeus](#)) [T.A.Christensen](#).

82 The segregate genus *Neosiphonia* [M.-S.Kim & I.K.Lee \(Kim & Lee, 1999\)](#) has been widely  
83 accepted and is now the second largest in the Polysiphoniae (Guiry & Guiry, 2016). *Neosiphonia*

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(type species: *N. flavimarina* ~~M. S. Kim & I. K. Lee~~ from Korea) is characterized by the following features: (1) thalli erect with a main axis bearing branches; (2) branches or trichoblasts formed on every segment; (3) rhizoids cut off from pericentral cells; (4) carpogonial branches 3-celled; (5) spermatangial branches formed on a branch of modified trichoblasts; (6) tetrasporangia in ~~a~~ spiral arrangement (Kim & Lee, 1999). These features contrast markedly with the key characters of *Polysiphonia sensu stricto*, exemplified by the type species *P. stricta* ~~(Dillwyn) Greville~~: prostrate axes with rhizoids in open connection with pericentral cells; carpogonial branches 4-celled; spermatangial branches borne directly on axes; tetrasporangia in straight rows (Kim *et al.*, 2000). In addition to describing the new species *N. flavimarina*, Kim & Lee (1999) also transferred eleven species of *Polysiphonia* to *Neosiphonia*, all based on material from Korea, and there are 43 currently recognized species (Guiry & Guiry, 2016), not all of which exhibit the six key characters of *Neosiphonia* listed above.

Kim & Lee (1999) considered *Neosiphonia* (also referred to as the "*Polysiphonia japonica* complex" *sensu* Yoon (1986)) to be related to *Fernandosiphonia* Levring, which was erected for *F. unilateralis* Levring from the Juan Fernández Islands off Chile on the basis of its unilateral development of ultimate branches (Levring, 1941) and which currently consists of three species. They reported that *Neosiphonia* differed from *Fernandosiphonia* principally in its branching pattern, the origin of spermatangial branches, and the 3-celled carpogonial branches. Kim & Lee (1999) did not comment, however, on the possible relationship between *Fernandosiphonia* and *Streblocladia* F. Schmitz (in Schmitz & Falkenberg, 1897). Hommersand (1963) and Norris (1994) compared *Fernandosiphonia* (trichoblasts formed spirally) with *Streblocladia* (trichoblasts borne only adaxially). Choi *et al.* (2001) drew attention to the relationship in their 18S tree between *N. japonica* ~~(Harvey) M. S. Kim & I. K. Lee~~ and *Polysiphonia virgata* ~~(C. Agardh) Sprengel~~, the type species of *Carradoriella* P.C.Silva (Kylin, 1956, as *Carradoria*; Silva *et al.*, 1996), and suggested that *Neosiphonia* might either be subsumed into *Carradoriella* or be resolved as a sister to it. Recent searches of DNA sequence databases unexpectedly showed a possible relationship between

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110 | *Neosiphonia* species and *Melanothamnus somalensis* ~~Bornet & Falkenberg~~, the type species of the  
111 | genus *Melanothamnus* ~~Bornet & Falkenberg~~ (~~in Falkenberg, 1901~~), which was regarded as  
112 | *incertae sedis* ~~by Bornet & Falkenberg in~~ (Falkenberg, 1901).

113 |         Given the taxonomic and nomenclatural complexity within the Polysiphonieae, our aims  
114 | were to re-evaluate the morphological features of *Neosiphonia* and *Vertebrata* in relation to those  
115 | of *Fernandosiphonia*, *Streblocladia*, *Carradoriella*, *Melanothamnus* and *Polysiphonia sensu*  
116 | *stricto* within a phylogenetic analysis of the Polysiphonieae using sequences of the plastid-encoded  
117 | *rbcL* gene and the ribosomal DNA 18S gene (SSU). We surveyed within the Polysiphonieae the  
118 | distribution of a striking characteristic of the "*Polysiphonia japonica* complex", the position of  
119 | plastids on radial walls of the periaxial cells and their absence from the outer walls such that nuclei  
120 | are clearly visible after staining (Maggs & Hommersand, 1993; McIvor *et al.*, 2001). Likewise, we  
121 | analysed the multinucleate vs. uninucleate character of trichoblast cells, which seems to be  
122 | taxonomically significant (Maggs & Hommersand, 1993).

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## 125 | MATERIALS AND METHODS

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127 | Field collections, morphological studies and literature review

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129 | Samples of Polysiphonieae (Table S1) were collected from European Atlantic coasts, New  
130 | Zealand, Australia, Taiwan, Japan, Chile, USA, South Africa and Oman and processed fresh,  
131 | desiccated in silica gel or preserved in ethanol.

132 |         Type material of *Fernandosiphonia unilateralis* ~~Levring~~ was obtained from the Herbarium,  
133 | Botanical Museum, Göteborg, Sweden (GB) by correspondence with the curator. It consisted ~~in~~ of  
134 | four permanent slides, a herbarium sheet and ~~formalin~~ liquid-preserved material. Furthermore, we  
135 | studied recent collections from Juan Fernández Islands, the type locality. We also studied the type

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136 material in US and TCD of several species currently assigned to *Neosiphonia* (Table S2;  
137 herbarium abbreviations as in Thiers, 2016) for which the key morphological characteristics (Table  
138 1) could not be clearly ascertained from published literature, in order to determine their correct  
139 generic assignment. For this purpose, we exclusively considered the descriptions provided for  
140 material from type localities or near them. To ensure the accuracy of our interpretation of the  
141 genera, our concept of them is based on material of their type species obtained from their type  
142 localities. For *Strebl cladia*, we used material of, and sequences from, the type species *S.*  
143 *glomerulata* (Montagne) Papenfuss from New Zealand. *Carradoriella* (i.e. *Polysiphonia virgata*)  
144 was obtained from the type locality in South Africa, and the type species of *Vertebrata* and  
145 *Melanothamnus* came from Ireland and Oman respectively.

146 Fresh material and herbarium samples were prepared as squashes, either unstained or stained  
147 with aqueous aniline blue, post-fixed in 1% HCl, and mounted in 80% Karo corn syrup (Bestfoods  
148 Inc, NJ, USA). Permanent slide mounts were prepared as vouchers and deposited in: BM, MICH,  
149 SANT, WNC and MEL.

150 A systematic review was carried out to identify relevant phycological literature from  
151 around the world from which to assess for each species of Polysiphonieae the 14 vegetative and  
152 reproductive features relevant to *Neosiphonia* and *Vertebrata*.

153 [Nomenclatural authorities for the species mentioned in the manuscript are provided in](#)  
154 [Tables 2-5 and S1-S2.](#)

156 DNA extraction, PCR amplification and sequencing

158 This was carried out in four different laboratories using different protocols as described below.

159 At Queen's University Belfast, DNA was extracted from fresh, silica gel-dried or ethanol-  
160 preserved material using the Qiagen DNeasy Plant Mini Kit (Qiagen GmbH, Hilden, Germany),  
161 according to the manufacturer's instructions, or by a CTAB method, modified after Doyle & Doyle



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(1987). For PCR amplification, a PTC-200 DNA Engine (MJ Research Inc.) was used. Except for material of *Fernandosiphonia unilateralis*, all PCR amplifications were carried out using *rbcLFC* as the forward primer, and *rbcLRD* as the reverse primer (Nam *et al.*, 2000; McIvor *et al.*, 2001). All reactions contained 200  $\mu$ M each of dATP, dCTP, dGTP and dTTP, 0.3  $\mu$ M of each primer, 2.5 mM MgCl<sub>2</sub>, and 1.6 units of Biotaq™ DNA Taq-polymerase (Bioline, UK). The PCR amplification followed Nam *et al.* (2000) and McIvor *et al.* (2001). About 1250 base pairs (bp) of the *rbcL* gene were amplified using ~~*rbcLFC* and *rbcLRD*~~ and ~~t~~. The PCR fragments for sequencing were purified using the High Pure PCR Product Purification Kit (Roche Diagnostics Ltd., Lewes, UK), according to the manufacturer's instructions. The PCR products were directly sequenced commercially by MWG-Biotech, Ebersberg, Germany.

Type material of *Fernandosiphonia unilateralis* had been preserved in formalin by Levring (1941) prior to long-term storage in ethanol (A. Athanasiados, personal communication). At the Leiden herbarium, various protocols for retrieving DNA from formalin-preserved specimens were attempted (Kirby & Reid, 2001); the most successful was to soak and wash the material repeatedly in clean sterile water, prior to DNA extraction using using a Chelex-100 (Biorad, Hercules, California) protocol (Goff & Moon, 1993; Zuccarello *et al.*, 1999). Applying a strategy for amplifying degraded "ancient" DNA (Provan *et al.*, 2008), primers were designed from an alignment of *Neosiphonia harveyi* (Bailey) M. S. Kim, H. G. Choi, Guiry & G. W. Saunders and related species in order to amplify 100-bp fragments. We used the primers F183 (5' TGCAGGTGAATCTTCTACAGCT 3') and R383 (5' ACGTTACCAATAATTGAAGCTGTT 3').

At the University of Melbourne, DNA was extracted from silica gel-dried material following Saunders & McDevit (2012). PCR amplification was carried out for *rbcL* using the primers F7/RrbcStart or F57/rbcLrevNEW (Freshwater & Rueness, 1994; Saunders & Moore, 2013) and for 18S using the primers F47 (5' AGCCATGCAAGTGCCTGTAT 3') and R1867 (5'CGCAGGTTACCTACGGAAA 3'). Reactions were performed in a total volume of 25  $\mu$ l,

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188 consisting of 5  $\mu$ l 5 $\times$  MyTaq<sup>TM</sup> reaction buffer, 0.7  $\mu$ l 10  $\mu$ M of forward and reverse primers,  
189 0.125  $\mu$ l 1U  $\mu$ l<sup>+</sup> My Taq<sup>TM</sup> DNA Polymerase (Bioline), 17.475  $\mu$ l MilliQ<sup>®</sup> water and 1  $\mu$ l  
190 template DNA. The PCR profile consisted of initial denaturation (93°C for 3 min); 35 cycles of  
191 denaturation (94°C for 30 s), primer annealing (45°C for 30 s), and extension (74°C for 90 s); and  
192 final extension (74°C for 5 min). The PCR products were purified and sequenced commercially by  
193 Macrogen.

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194 At A Coruña, *Melanothamnus* from Oman was extracted using the CTAB protocol (Doyle  
195 & Doyle, 1987) and *rbcL* was amplified using the primers F7-R753 and F57-rbcLrevNEW  
196 (Freshwater & Rueness, 1994; Saunders & Moore, 2013). The PCR products were purified and  
197 sequenced commercially by the sequencing service of the University of A Coruña.

198 DNA extraction, amplification and sequencing at UNCW were as described by Stuercke &  
199 Freshwater (2008).

200  
201 Sequence alignment and phylogenetic analysis

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203 A total of 65 *rbcL* and 48 18S sequences were downloaded from GenBank and 25 new *rbcL* and  
204 ten new 18S sequences were generated in this study. The sequences and their corresponding  
205 GenBank accession numbers are listed in Table S1.

206 Sequences were aligned using Muscle in Geneious 6.1.8 (Kearse *et al.*, 2012). Identical  
207 sequences and those that diverged by less than 1.1% were removed from the *rbcL* analysis, except  
208 for *Neosiphonia flavimarina* and *N. harveyi* (0.4% divergence), the two selected representatives of  
209 the “*N. japonica* complex” (Kim & Lee, 1999), which also includes *N. decumbens*, *N. harlandii*  
210 and *P. akkeshiensis* [Segi](#) (McIvor *et al.*, 2001; Kim & Yang, 2006; Savoie & Saunders, 2015;  
211 Bárbara *et al.*, 2013). Identical sequences were also removed from the 18S analysis. The sequences  
212 included in the final alignment were selected after considering their quality in terms of both length  
213 and the presence of ambiguous bases. Phylogenetic trees for *rbcL* and 18S were estimated with

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214 Maximum Likelihood (ML) using RAxML 8.1.6 (Stamatakis, 2014). GTR-Gamma was selected as  
215 the best nucleotide model; branch support was estimated with 100 bootstrap replicates. Three  
216 species of *Symphyocladia* [Falkenberg \(in Schmitz & Falkenberg, 1897\)](#) were selected as the  
217 outgroup in the *rbcL* phylogeny and one species each of *Symphyocladia*, [Xiphosiphonia Savoie &  
218 Saunders \(2016\)](#) *Pterosiphonia* [Falkenberg \(in Schmitz & Falkenberg, 1897\)](#) and *Herposiphonia*  
219 [Nägeli \(1846\)](#) were selected as outgroups for the 18S analysis. This outgroup selection was based  
220 on our phylogenomic analyses of the major lineages of the Rhodomelaceae which resolve a clade  
221 formed by the Herposiphonieae and Pterosiphonieae as sister to the Polysiphonieae (Díaz-Tapia *et*  
222 *al.*, 2015).

223 We used MrBayes v.3.2.2 for Bayesian phylogenetic inference (Ronquist *et al.*, 2011). The  
224 *rbcL* alignment was analysed using a single (unpartitioned) GTR+ $\Gamma$ +I as well as completely  
225 unlinked GTR+ $\Gamma$ +I for each codon position. We used a single GTR+ $\Gamma$ +I model for 18S. All  
226 analyses were run for ~~5M millions of~~ generations, sampling every 1,000th generation and using  
227 two independent runs each consisting of four incrementally heated Metropolis-coupled (MCMC)  
228 chains. Convergence and stationarity of runs were evaluated with Tracer v.1.6.0 (Rambaut *et al.*,  
229 2013), resulting in the use of a burnin of 500k generations for all analyses. Post-burnin trees were  
230 summarized with the `sump+` command in MrBayes, using the all-compatible-groups consensus  
231 type.

232 Trees were calibrated in geological time using relaxed molecular clock analyses. The  
233 calibration was derived from node ages inferred by Yang *et al.* (2016), which estimated the earliest  
234 split in Ceramiales (between *Spyridia* [Harvey \(1833\)](#) and the remaining Ceramiales) to be 292 Ma  
235 old (stdev  $\approx$  24.6 Ma). After adding the *rbcL* sequences of Ceramiales from the Yang *et al.* (2016)  
236 study to our alignment and setting *Spyridia* as the outgroup, node ages were inferred with two  
237 Bayesian methods. The first analysis used an autocorrelated model of molecular evolutionary rate  
238 change (Thorne & Kishino, 2002) as implemented in PhyloBayes v.3.3f (Lartillot *et al.*, 2009).  
239 The MCMC chain was run for 50k cycles, stationarity was assessed with Tracer, and the node ages

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summarized with the readdiv command, discarding the first 25k cycles as burnin. The second analysis used uncorrelated rates of evolution sampled from a lognormal distribution (Drummond *et al.*, 2006) as implemented in BEAST v.1.8.2. The MCMC chain was run for 10 ~~M~~-million generations, used a Yule tree prior, and an unpartitioned GTR+ $\Gamma$ +I model of sequence evolution. Stationarity was assessed with Tracer. A maximum clade credibility tree and median node heights were inferred with TreeAnnotator, discarding the first ~~1M~~-1 million generations as burnin and using a posterior probability limit of zero.

## RESULTS

### DNA sequences and alignments

DNA extraction and PCR amplification of type material of *Fernandosiphonia unilateralis* that had been initially ~~formalin~~Formalin/seawater fixed and then stored in ethanol for several decades yielded a 95 bp partial *rbcL* sequence with seven ambiguous nucleotides. The sequence was unique by comparison with other taxa sequenced either at QUB or in Leiden, confirming that there had been no contamination.

25 new *rbcL* sequences and ten 18S sequences were obtained from members of the Polysiphoniae (Table S1), including an *rbcL* sequence from *Melanothamus somalensis*, and four *rbcL* and two 18S sequences from new collections of *F. unilateralis* from the type locality.

Alignments for the *rbcL* were unambiguous, with no insertions or deletions.

### Phylogenetic analyses

The ML *rbcL* tree (Fig. 1) has three strongly supported major clades within the Polysiphoniae: *Polysiphonia sensu stricto* 1 (including *P. stricta*, the type of the genus), *Polysiphonia sensu stricto* 2 (with morphological features corresponding to those defining *Polysiphonia sensu stricto*:

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Kim *et al.*, 2000) and a third clade grouping all the other taxa. The third clade comprised a large number of lineages, many with low or intermediate support. The two most speciose lineages, here named *Vertebrata* and *Melanothamnus*, however, are both robustly supported (Fig. 1). The *Vertebrata* clade includes *V. lanosa*, the current name for the type species of *Vertebrata*, *V. fastigiata* S.F.Gray (1821), as well as the type species of several other genera: *Brongniartella* Bory (1822), *Boergeseniella* Kylin (1956), *Enelittosiphonia* Segi (1949) and *Ctenosiphonia* Falkenberg (in Schmitz & Falkenberg, 1897). The *Melanothamnus* clade includes *Fernandosiphonia unilateralis*, *Neosiphonia flavimarina*, and *M. somalensis*, the type species of their corresponding genera. In addition to these two large clades, six other lineages containing 3-4 species are highly supported (BP/PP > 94/0.95); among these are the *Carradoriella* clade including *Polysiphonia virgata*, the type species of *Caradoriella*, and the *Streblocladia* clade, which includes the type species *S. glomerulata*. Our phylogenetic tree also resolved five individual species as sisters to the other clades with low support.

The *Melanothamnus* clade receives support of 100/1.00 (Fig. 1). In addition to *F. unilateralis*, *N. flavimarina* and *M. somalensis*, this clade includes 27 other species currently assigned to *Neosiphonia* and *Polysiphonia*. The 95 bp sequence obtained from the type material of *F. unilateralis* analysed separately showed that this sequence was positioned unequivocally within the *Melanothamnus* clade, but sequence ambiguities due to the quality of the DNA made it impossible to determine its precise position.

The phylogenetic relationships among species within the *Melanothamnus* clade are generally poorly resolved, with a few exceptions. Although the lineage formed by "*Polysiphonia*" *schneideri*, "*P.*" *amplacapilli*, "*P.*" *pentamera* and "*P.*" *morroides* is very weakly positioned as sister to the *Melanothamnus* clade in the *rbcL* tree, in 18S analyses this position is robustly supported (see below).

The RAxML 18S tree (Fig. 2) has a similar topology to the *rbcL* phylogeny, with three strongly supported major clades: *Polysiphonia sensu stricto* 1 and 2 and a third clade with all the

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292 other taxa. *Polysiphonia sensu stricto* clades 1 and 2 are placed robustly together (99/1.00). Within  
293 the third clade, the *Vertebrata* clade receives full support, while support is lower for  
294 *Melanothamnus* (82/1.00). The sister relationship between the *Melanothamnus* and "P."  
295 *schneideri* clades is strongly supported in the 18S phylogeny. In addition, the *Carradoriella* and  
296 *Streblacladia* clades are highly supported.

297 The time-calibrated phylogenies (Figs S1, S2) estimated the divergence in *Vertebrata* to be  
298 more ancient than in *Melanothamnus* (90.7-138.66 vs 75.7-95.78 Ma). Furthermore, the radiation  
299 of major lineages in *Vertebrata* and *Melanothamnus* was gradual and took place over periods of  
300 ca. 20 and 12 Ma, respectively.

302 Morphological observations

304 An overview of the distribution of selected morphological characters within clades of the  
305 Polysiphonieae is shown in Table 1.

307 *Habit*: There is considerable variation within and among clades (Table 1), with the exception of  
308 the *Carradoriella* clade, in which both species are erect. True prostrate axes giving rise to erect  
309 axes, as opposed to decumbent axes that themselves become erect, are confined to *Polysiphonia*  
310 *sensu stricto* and *Vertebrata*. Most species of the *Melanothamnus* clade are completely erect or  
311 have a very short prostrate system. However, some taxa are decumbent (e.g. *Polysiphonia blandii*,  
312 *P. simplex*), forming extensive prostrate systems with rhizoids in the basal parts of the erect axes.  
313 Members of the Polysiphonieae are typically smaller than 10 cm. As an exception, *M. afaqhusainii*  
314 can exceed 1 m in length.

316 *Rhizoids*: The connection between the rhizoids and the pericentral cells from which they originate  
317 is a uniform character within each clade, so far as it can be observed (Table 1). Rhizoids are in

14

open connection with pericentral cells in *Polysiphonia sensu stricto* (Fig. 19), while they are cut off from pericentral cells in the other clades (Figs 20-24). Observations on rhizoids cannot be made in mature specimens of some species, such as *Vertebrata lanosa* which is an obligate hemiparasite that lacks rhizoids, and *Fernandosiphonia unilateralis*, *Streblocladia glomerulata* and *Melanothamnus somalensis*, which all have compact basal discs without individual rhizoids.

*Pericentral cells and cortication:* The number of pericentral cells and the presence of cortication are variable in most of the clades (Table 1). All species in the *Vertebrata* clade have six or more pericentral cells, while members of the *Polysiphonia sensu stricto* clades have four pericentral cells, with the exception of *Bryocladia cuspidata* (6-8 pericentrals). Cortication is uniformly absent in the *Polysiphonia sensu stricto* and "*P.*" *schneideri* clades. Cortication is variable within the other clades, absent or slight in small species of *Fernandosiphonia* but very heavy in *Melanothamnus*, and absent or slight in most species of *Vertebrata* with the exception of *Boergeseniella*, in which cortication is elaborate.

*Plastid arrangement:* The arrangement of plastids in the cells is a synapomorphy for the *Melanothamnus* clade. The species in this clade have the plastids lying exclusively on radial walls of pericentral cells so the outer walls appear transparent (Table 1, Figs 8, 13, 34-39). This particular arrangement of the plastids can be easily observed under the microscope as the cells show a dark flank when observed in detail (Figs 14, 35, 37), as well as a transparent halo when the pericentral cells are observed in a suitable position (Fig. 38). All the other taxa of the Polysiphonieae have plastids against all the cell walls including the outer wall (Table 1, Figs 25-33). The revision of the type materials listed in Table S2, currently assigned to *Neosiphonia*, allowed us to verify the plastid character in the species *Polysiphonia concinna*, *P. eastwoodiae*, *P. gorgoniae*, *P. harlandii* and *P. johnstonii*. Conversely, the species *Lophosiphonia mexicana*, *P.*

15

343 *beaudettei*, *P. confusa*, *P. poko*, *P. profunda* and *P. rubrorhiza* have the plastids scattered within  
344 the cells, including against the outer wall cells.

345

346 *Branch/trichoblast arrangement*: Whether trichoblasts and/or branches are formed on every

347 segment or are separated by naked segments is variable in three clades, *Melanothamnus*,

348 *Carradoriella* and *Vertebrata*. Most species of the *Melanothamnus* clade have branches or

349 trichoblasts on every segment, which is a key feature of *Neosiphonia*. However, there are

350 exceptions in this clade such as *Neosiphonia collabens*, *Polysiphonia nuda* and *P. pseudovillum*

351 from Panama, in which there are interspersed naked segments. Conversely, the formation of

352 trichoblasts/branches with naked segments between them is a uniform character in the

353 *Streblacladia*, "*Polysiphonia*" *schneideri* and *Polysiphonia sensu stricto* clades (Table 1). Within

354 all clades except *Melanothamnus*, branches may form in a position axillary to trichoblasts, but

355 although constant at the species level, this character is variable within clades. In the

356 *Melanothamnus* clade this character is absent, and branches are never axillary.

357

358 *Trichoblast nuclei*: The proximal cells of trichoblasts are multinucleate in the *Vertebrata* clade

359 (Table 1, Figs 41-43), with up to 8 or more nuclei in the basal cell and decreasing in number

360 towards the apices, which can be uninucleate. The nuclei are uniformly distributed inside the cells,

361 each appearing to have a domain within the cell. Conversely, all the cells of trichoblasts are

362 uninucleate in other clades of the Polysiphonieae (Figs 40, 44-46). The only known exception is

363 *Leptosiphonia schousboei*, which sometimes has two nuclei in the trichoblast cells.

364

365 *Branching pattern*: Despite the great significance previously placed on dorsiventral vs. radial

366 branching in the Rhodomelaceae, this character varies within all our clades. A primary dorsiventral

367 branching pattern characterizes some species of the clades *Melanothamnus* (*F. unilateralis* and *N.*

368 *collabens*; Figs 10, 11), *Streblacladia* (*S. glomerulata*) and *Vertebrata* (*Ctenosiphonia hypnoides*)



16

(Table 1). However, this characteristic is not significant in delineating these three genera, as our phylogenetic tree reveals that each of these four species is closely related to others that have spirally or pseudodichotomously arranged branches. For example, the branching pattern of members of the *Streblocladia* clade varies from dorsiventral in *S. glomerulata*, the type species, to spiral or pseudodichotomous in *Polysiphonia muelleriana* and *Polysiphonia* sp. Likewise, the dorsiventral *Neosiphonia collabens* is related to species with spiral or pseudodichotomous branching patterns.

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*Spermatangial branches*: Whether spermatangial branches replace trichoblasts completely or replace only one branch of a dichotomously branched trichoblast is a constant character in all clades (Table 1). In the two *Polysiphonia sensu stricto* and *Streblocladia* clades, spermatangial branches almost uniformly replace trichoblasts (Fig. 47). In the other clades, they are formed on the first dichotomy of modified trichoblasts (Figs 15, 49-52), with the exception of *Vertebrata* (Fig. 48) as *V. lanosa* has no trichoblasts in male thalli - they can only be observed occasionally in females. The presence or absence of apical sterile cells on spermatangial branches is variable within clades, except for *Carradoriella* in which they are present (Figs 47-52, Table 1).

*Carpogonial branches*: The *Melanothamnus* clade is characterized by having 3-celled carpogonial branches (Table 1). In our study, we observed this character in *N. harveyi*, *N. collabens*, *P. blandi* and *P. forfex* (Figs 57, 58). By contrast, the other Polysiphonieae uniformly have 4-celled carpogonial branches like the majority of the Rhodomelaceae (Table 1, Figs 53-56).

*Cystocarps*: The outline morphology of cystocarps varies from globose to ovoid in all the clades analysed here (Table 1, Figs 60-64). Urceolate cystocarps are exclusive to the *Polysiphonia sensu stricto* clades (Table 1, Fig. 59). Cells around the ostiole are conspicuously larger than (more than twice the size of) the cells of the pericarp immediately below in most species of the

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395 *Melanothamnus* clade (Fig 70). However, *Neosiphonia harveyi* is an exception, and the cells of  
396 the ostiole in this species are only slightly larger than the other cells of the pericarp. This character  
397 is also seen in *Streblocladia glomerulata* (Fig. 68). Conversely, the cells of the ostiole in the other  
398 four clades are uniformly similar to the cells below (Figs 65-67, 69).

399  
400 *Tetrasporangia*: The formation of tetrasporangia in straight or spiral rows is variable in all clades  
401 (Table 1, Figs 71-76). It must be noted that very long straight series of tetrasporangia are typically  
402 observed only in members of the *Polysiphonia sensu stricto* clade (Fig. 71). However, straight  
403 series can also form in other clades, for example in *Neosiphonia collabens* and *Polysiphonia nuda*  
404 within the *Melanothamnus* clade whereas tetrasporangia in *Fernandosiphonia unilateralis* form  
405 short and markedly spiral series (Fig. 18). The third tetrasporangial cover cell is exclusive to the  
406 *Polysiphonia sensu stricto* clade, but this character has not been examined in all the species.

407

408

## 409 DISCUSSION

410

### 411 Phylogenetic analysis

412 Amongst the Polysiphonieae studied here, the early-branching clade/clades *Polysiphonia sensu*  
413 *stricto* 1 and 2 were resolved as separate lineages in *rbcL* analyses (Fig. 1) but together formed a  
414 robust clade in 18S analyses (Fig. 2). The marked discordance between *rbcL* and 18S trees  
415 regarding the monophyly/paraphyly of the *Polysiphonia sensu stricto* lineages requires additional  
416 research for a more accurate assessment of relationships and character evolution. Because the  
417 *Polysiphonia sensu stricto* lineages occur near the base of the tree, it is possible that the outgroups  
418 (which are relatively distant taxa compared to the ingroup) could have attached to the ingroup in  
419 the wrong position in one of the analyses (Shavit *et al.*, 2007). Future work should focus on

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including a wider range of taxa from across the Rhodomelaceae as well as using larger, multi-gene datasets to infer the correct branching order of the two *Polysiphonia sensu stricto* lineages.

The *Vertebrata* and *Melanothamnus* clades were resolved as large, speciose clades with strong support using *rbcL*. The 18S phylogeny also resolves the *Vertebrata* clade with robust support, while *Melanothamnus* is moderately well supported. Both clades are clearly distinguished from *Polysiphonia sensu stricto* by the rhizoid anatomy (cut off from pericentral cells). Both clades are identified by distinct morphological synapomorphies. The *Vertebrata* clade is characterized by the multinucleate cells of trichoblasts; the other key feature of *Vertebrata*, that all species have six or more pericentral cells, is shared with members of some other clades. The *Melanothamnus* clade is unequivocally distinguished from other Polysiphonieae by two synapomorphic characteristics: the plastid arrangement and the 3-celled carpogonial branches. Furthermore, branch origin is independent from trichoblasts in all the species of this clade, and the majority of species have enlarged ostiolar cells.

In addition to the above-mentioned clades, the *rbcL* phylogeny resolved six small (3-4 species) but highly supported clades, as well as indicating five species that are uncertainly positioned. The generic assignment of these lineages requires further taxon and gene sampling in order to better understand their phylogenetic relationships and establish a natural classification – [it would be premature to speculate on the outcomes of these investigations at present](#). One of the major shortcomings in Polysiphonieae sequence databases is the uneven geographical sampling, as the majority of sequenced taxa come from Atlantic Europe and northwestern America. The generation of molecular data from additional regions could contribute to acquiring a more realistic perspective of the magnitude of unplaced lineages and to delineating their corresponding genera. Also, the resolution of the commonly employed molecular markers in the Polysiphonieae is not sufficient to resolve the phylogenetic relationships among numerous lineages, which could be improved using larger gene datasets (Díaz-Tapia *et al.*, 2015).

19

**Taxonomic position of *Vertebrata***

*Vertebrata lanosa* is placed in a strongly supported clade that also includes *Brongniartella byssoides*, *Boergeseniella fruticulosa*, *Ctenosiphonia hypnoides* and *Enelittosiphonia stimpsonii*, the type species of their corresponding genera, and *Lophosiphonia reptabunda* (which is not the type species). All members of this clade have a synapomorphic characteristic that was previously overlooked in relation to systematics (but see Maggs & Hommersand, 1993): multinucleate trichoblast cells. We conclude from molecular and morphological evidence that members of this clade represent a single genus. *Vertebrata* is the oldest name among those available for this clade, as noted before (Choi *et al.*, 2001), and the new combinations proposed in Table 2 are required. Furthermore, the *Vertebrata* binomials previously established by Kuntze (1891) should be reinstated for the other 13 species included in this clade (Table 3).

Interestingly, *Brongniartella* is not monophyletic despite its distinctive persistent and pigmented trichoblasts that led to its classification in the tribes Lophothalieae (Falkenberg, 1901; Womersley, 2003) or Brongniartelleae [Parsons](#) (Parsons, 1975; Maggs & Hommersand, 1993). Although trichoblasts are typically considered unpigmented in the Polysiphonieae, they are commonly pigmented when young before they enlarge and become colourless (Delivopoulos, 2002). The two currently recognized species of *Brongniartella*, *B. byssoides* and *B. australis*, were separated within the *Vertebrata* clade, respectively placed with *V. lanosa* and *Polysiphonia nigra*.

*Ctenosiphonia* is a monotypic genus segregated from *Polysiphonia* due to its very peculiar morphological characteristics, including a dorsiventral thallus and two tetrasporangia per segment (Falkenberg, 1901; Díaz-Tapia & Bárbara, 2013). This genus, together with *Lophosiphonia* [Falkenberg \(1987\)](#), is currently positioned within the “Lophosiphonia group” (Falkenberg, 1901). *Boergeseniella* and *Enelittosiphonia* were distinguished from other Polysiphonieae by their particular branching patterns (Kylin, 1956; Segi, 1949), but our molecular evidence (Fig. 1) does not support their recognition as independent genera.

20

472 The diversity of currently recognized genera included in this clade reflects the high  
473 variability among *Vertebrata* species in trichoblast characteristics (pigmented/unpigmented;  
474 persistent/deciduous; spirally/dorsiventrally arranged) and branching patterns (spiral/dorsiventral;  
475 presence or absence of alternating branches of determinate and indeterminate growth), which  
476 classical authors considered important at levels of genus and tribe (Falkenberg, 1901; Kylin, 1956;  
477 Hommersand, 1963).

478 The main morphological character delineating the *Vertebrata* group is that trichoblast cells  
479 are multinucleate. In the Polysiphonieae and some other Ceramiales, the apical cell is uninucleate,  
480 whereas the cells cut off from it undergo nuclear divisions during elongation, becoming  
481 multinucleate, with the number of nuclei being proportional to the volume of the cell (Goff &  
482 Coleman, 1986; McIvor *et al.*, 2002). The trichoblasts of the Rhodomelaceae are usually  
483 uninucleate, whereas the polysiphonous parts of the thalli are multinucleate (Coomans &  
484 Hommersand, 1990; Garbary & Clarke, 2001; Delivopoulos, 2002). A plausible advantage of  
485 having multinucleate trichoblasts in *Vertebrata* is that their cells can reach larger sizes. In fact,  
486 trichoblasts in this genus are sometimes extremely well developed, exceeding 10 mm in length in  
487 species such as *Vertebrata (Lophosiphonia) reptabunda* and *V. (Ctenosiphonia) hypnoides*. In the  
488 red algae, cell streaming is slow compared with other algae (Pueschel, 1990), and multinuclearity  
489 of large cells may facilitate the regulation of cellular activities. Several potential functions have  
490 been attributed to the vegetative hairs of the red algae or trichoblasts of the Rhodomelaceae  
491 including desiccation resistance, nutrient uptake, metabolite secretion, shading, trapping of  
492 spermatia, mucilage stabilization and monitoring of phosphorus status (Delivopoulos, 2002, and  
493 references therein). Physically, trichoblasts can form a dense network around the apices that could  
494 potentially restrict access to the cells by small grazers, such as amphipods and copepods.

495  
51 **Taxonomic position of *Neosiphonia*, *Fernandosiphonia* and *Melanothamnus***  
52

21

497 The presence of the type species of the genus *Melanothamnus* (*M. somalensis*) in a strongly  
498 supported clade with the type species of the genus *Neosiphonia* (*N. flavimarina*) and  
499 *Fernandosiphonia* (*F. unilateralis*) indicates that *Neosiphonia*, *Fernandosiphonia* and  
500 *Melanothamnus* are not distinct monophyletic genera. *Neosiphonia* is a later heterotypic synonym  
501 of *Fernandosiphonia*. However, the name *Melanothamnus* is older than both *Fernandosiphonia*  
502 and *Neosiphonia*, and the new combinations proposed in Tables 4 and 5 are required. These new  
503 combinations include 31 species that were previously assigned to *Neosiphonia*; two species known  
504 to be closely related to *Neosiphonia* but that had been retained in *Polysiphonia* because their  
505 morphology conflicted with Kim & Lee (1999); six species for which molecular data are presented  
506 here for the first time; and three species that are transferred to *Melanothamnus* on the basis of their  
507 morphology.

508 On the other hand, ten species that are currently placed in *Neosiphonia* should be replaced in  
509 *Polysiphonia* for formal purposes pending clarification of their phylogenetic affinities and generic  
510 assignment. *Polysiphonia beaudettei*, *P. confusa*, *P. echinata*, *P. elongella*, *P. poko*, *P. rubrorhiza*  
511 and *P. profunda* were assigned to *Neosiphonia* based on morphological characteristics (Kim &  
512 Lee, 1999; Abbott *et al.*, 2002; Kim & Abbott, 2006; Mamoozadeh & Freshwater, 2011; Norris,  
513 2014). However, they lack the plastid character, and furthermore molecular data for *P. echinata*  
514 and *P. elongella* show that they do not belong to the *Melanothamnus* clade (Fig. 1). Likewise,  
515 *Polysiphonia sertularioides* was transferred to *Neosiphonia* based on the morphology of Korean  
516 material attributed to this species (Nam & Kang, 2012). However, its type locality is in the  
517 Mediterranean, and Atlantic sequences for this species are not in the *Fernandosiphonia* clade (Fig.  
518 1; Mamoozadeh & Freshwater, 2012). *Polysiphonia paniculata* was transferred to *Neosiphonia*  
519 (Norris, 2014), but again it is not in the *Melanothamnus* clade (Figs 1, 2). Finally, our study of the  
520 type material of *Lophosiphonia mexicana*, also transferred to *Neosiphonia* (Norris, 2014; Table  
521 S2), leads us to conclude indicates that this species is probably not a member of the  
522 Polysiphonieae. As noted by Norris (2014), further studies are needed to clarify the generic

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523 placement of this unusual species, and meanwhile we propose to leave it in *Lophosiphonia* until  
524 more information is available.

525 Specimens of *Melanothamnus* collected in Oman and housed in MICH were initially  
526 assigned to *M. somalensis* (Wynne & Banaimoon, 1990), before the description of *M. afaqhusainii*  
527 ~~M. Shameel~~ from Pakistan (1999). Revision of the Omani materials leads us to conclude that both  
528 *M. somalensis* and *M. afaqhusainii* are represented in Oman, and their morphology agrees with the  
529 criteria proposed by Shameel (1999, 2000) for distinguishing them. Their *rbcL* sequences diverged  
530 by 1.4% (18 bp).

531 The *Melanothamnus* clade is morphologically distinguished from other members of the tribe  
532 Polysiphonieae by an unequivocal synapomorphic character: plastids lie exclusively on the radial  
533 walls of the pericentral cells and are absent from outer walls. The plastid character was previously  
534 noted by Hollenberg (1961, 1968a), who described “hyaline cell walls” for several species (e.g. *P.*  
535 *pseudovillum*, *P. bajacali*), and by Maggs & Hommersand (1993). However, its significance at  
536 higher taxonomic levels has not previously been highlighted. We observed this character in a total  
537 of 35 species, and we conclude that it is uniform in the *Melanothamnus* clade. Conversely, other  
538 Polysiphonieae and most of the Rhodomelaceae have plastids distributed within the cytoplasm,  
539 some lying against outer cell walls. In the family, the only other exception is some species of  
540 *Herposiphonia* in which the plastids form transverse bands (Hollenberg, 1968c; Womersley, 2003;  
541 Díaz-Tapia & Bárbara, 2013).

542 Carpogonial branches are typically 4-celled throughout the family Rhodomelaceae. 3-celled  
543 carpogonial branches were described for the first time in *Polysiphonia platycarpa* (Iyengar &  
544 Balakrishnan, 1950), and later this was one of the features proposed to delineate the genus  
545 *Neosiphonia* (Kim & Lee, 1999). 3-celled carpogonial branches have been reported in 17 species  
546 (four of them in the “*japonica*-complex”), all of which are placed here in *Melanothamnus*.  
547 Alternative interpretations of the carpogonial branch configuration were found in the literature for  
548 *F. unilateralis*, as Leving (1941) described and illustrated a 4-celled structure, while Morrill (1976,

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plate 37, figs E and H) illustrated 3-celled carpogonial branches in the same species, also from the type locality. This character can be easily misinterpreted if the carpogonial branches are not observed at the right developmental stage. In our study of the type material, a single procarp was observed in a permanent slide (Fig. 16), most probably the same one illustrated by Levring. It is unclear how this procarp should be interpreted because it is too mature, and so it is difficult to determine with certainty which cell corresponds to the sterile basal cell and which to the basal cell of the carpogonial branch. From the evidence of the presence of both the plastid character and 3-celled carpogonial branches, *Kintarosiphonia fibrillosa* Uwai & Masuda (1999), based on *Pterosiphonia fibrillosa*, and *Polysiphonia platycarpa* are also here transferred to *Melanothamnus* (Table 1).

The other morphological characters proposed by Kim & Lee (1999) to delineate the genus *Neosiphonia* vary among closely related species, except for the rhizoid anatomy. Rhizoids are cut off from the pericentral cells in all Polysiphonieae except for *Polysiphonia sensu stricto* in which they are in open connection with the pericentral cells. After the establishment of *Neosiphonia*, numerous species were transferred to the new genus based on morphology, but commonly overlooking the number of cells in carpogonial branches. Excluding this trait, several species have all five characteristics proposed by Kim & Lee (1999) to delineate *Neosiphonia* but nevertheless are not in the *Melanothamnus* clade (e.g. *P. brodiei*, *P. echinata*, *P. elongella*), while several species are clearly in the clade (e.g. *M. collabens*, *M. nuda*, *M. pseudovillum*) but lack this combination of traits.

The key morphological feature of *Melanothamnus* is the restriction of plastids to the radial walls of the pericentral cells and their absence from the outer walls. Algae demonstrate a notable decline in photosynthesis at higher light levels possibly due to damage to the photosynthetic apparatus caused by excessive light delivery to photosystem II (Lüning, 1990; Hurd *et al.*, 2014). Many green and brown algal plastids have phototropic reactions to blue and UV light in order to protect them from irradiation damage (Lüning, 1990). Plastid movement, however, has never been



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demonstrated for the vast majority of red algae (Pueschel, 1990), and it appears that red algae have evolved other types of protection against UV damage. Red algae including *Polysiphonia* species have high concentrations of various mycosporine-like amino acids that respond rapidly to environmental change and act as defences against the photooxidative effects of sunlight (Karsten *et al.*, 1998; Navarro *et al.*, 2014). The movement of the plastids onto the radial walls of the periaxial cells, in combination with MAAs, may have given the *Melanothamnus* ancestor a selective advantage over other Polysiphonieae, allowing it to exploit new ecological niches. The prevalence of *Melanothamnus* species in habitats with exposure to high light levels, such as in Hawaii or turfs on coral reefs (Price & Scott, 1992; Kim & Abbott, 2006), supports this speculation.

#### **Biogeography of *Vertebrata* and *Melanothamnus***

The genus *Vertebrata* is distributed worldwide and representatives have been described from all regions where there has been a detailed study of the tribe Polysiphonieae. The majority of our sequences are from Europe, but our systematic review and unpublished data suggest that this genus is widespread. BEAST and PhyloBayes calibrations indicate radiation of the major lineages of the *Vertebrata* clade over a 20 MA period starting about 140 or 90 Ma (estimates from different methods; see Figs S1, S2). Further conclusions as to its origins and centres of diversity would be premature, pending more comprehensive sampling.

In contrast, *Melanothamnus* is predominantly Indo-Pacific (Fig. 77). Although few molecular data are available from Indian coasts, some species occur in South Africa (*M. incompta*), Oman (*M. somalensis* and *M. afaqhusainii*), India (*M. platycarpa*) and Thailand (*M. thailandica*). Among the regions for which there is a comprehensive study of the Polysiphonieae, the diversity of *Melanothamnus* is particularly high in Korea, Japan and Hawaii (14, 11 and 14 species, respectively). This genus is also well represented on North American Atlantic coasts (4-5 species), but it is almost completely absent from Atlantic and Mediterranean Europe, where only

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two species have been reported, which are both most probably examples of old human-mediated introductions. *Melanothamnus harveyi* is native to southeastern Asia and has been introduced by multiple events onto northern Atlantic coasts (McIvor *et al.*, 2001; Savoie & Saunders, 2016). Similarly, *M. collabens* is likely to be an old introduction into the Atlantic, where it extends from the Bay of Biscay to Cape Verde, including the western Mediterranean (Díaz-Tapia & Bárbara, 2013). The finding of *M. collabens* in California (as *P. johnstonii*, see Table 4) supports this hypothesis, but [although \*Polysiphonia johnstonii\* was first collected from the Gulf of California in 1921 \(Setchell & Gardner, 1924\)](#), California was probably not the original source of the introduction. ~~[Polysiphonia johnstonii was first collected from the Gulf of California in 1921 \(Setchell & Gardner, 1924\)](#)~~. However an [An](#) investigation of *Polysiphonia* species from the Northern Gulf of California (Hollenberg & Norris, 1977) suggested that since its initial collection and description, *P. johnstonii* has extended its range along the Pacific coast of North America, fulfilling one of the criteria for an invasive species (Chapman & Carlton, 1991; Ribera & Boudouresque, 1995). How far this species has spread along the Pacific coast of America and along North Atlantic coastlines remains to be determined, and further sampling is needed to establish its origin.

The absence of naturally occurring *Melanothamnus* species in the Mediterranean and northeastern Atlantic might suggest that *Melanothamnus* is of recent origin, having evolved in the Pacific Ocean after the closure of the Tethys Seaway, between 60 and 20 million years ago, particularly as the sister "*P.*" *schneideri* clade is also primarily Pacific in distribution. In our *rbcL* phylogeny (Fig. 1), the "*P.*" *schneideri* clade includes two Korean species and two species distributed in the Pacific and North America with one of them introduced in Europe (Díaz-Tapia *et al.*, 2013). Furthermore, our surveys in Australia revealed five other Indo-Pacific species belonging to this clade (unpublished data). However, BEAST and PhyloBayes calibrations indicate radiation of the major lineages of the *Melanothamnus* clade over a 12 Ma period starting about 95 or 75 Ma (the two methods providing different estimates), with divergence from the "*P.*"

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627 *schneideri* clade 140 or 95 Ma (Figs S1, S2). The distribution resembles a Tethyan one that  
628 originated during the Cretaceous 125-75 Ma (Lüning, 1990; Hommersand, 2007) when the Tethys  
629 Ocean formed a tropical girdle around the earth. Unlike typical Tethyan distributions, in addition  
630 to its wide occurrence throughout the tropics, *Melanothamnus* occupies more temperate regions in  
631 the North Pacific (e.g. Japan, Korea) and the South Pacific/Oceania (e.g. South Australia, New  
632 Zealand). The question of whether *Melanothamnus* failed to colonize the northeastern Atlantic as it  
633 opened up during the Cretaceous, or whether northeastern Atlantic lineages evolved but became  
634 extinct, perhaps during Pleistocene glaciations, cannot be answered at present.

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638  
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Table 1. Comparison of selected morphological characteristics among the *Polysiphonia sensu stricto* 1 and 2, *Vertebrata*, *Carradoriella*, *Streblacladia*, *Polysiphonia schneideri* and *Melanothamnus* clades.

Feature	<i>Polysiphonia sensu stricto</i> 1 and 2	<i>Vertebrata</i>	<i>Carradoriella</i> clade	<i>Streblacladia</i> clade	<i>"Polysiphonia" schneideri</i> clade	<i>Melanothamnus</i>
Thallus habit	Erect; decumbent; prostrate	Erect; decumbent; prostrate	Erect	Erect	Erect; decumbent	Erect; decumbent
Rhizoid connection	Open	Cut off	Cut off	Cut off	Cut off	Cut off
Pericentral cells	4 (6-8 in <i>Bryocladia cuspidata</i> , clade 2)	6-24	5-16	4-12	4-7	4-9
Cortication	Absent	Absent / Present	Present	Present	Absent	Absent / Present
Plastid arrangement	Scattered	Scattered	Scattered	Scattered	Scattered	Radial walls
Branch/trichoblast arrangement	With naked segments	On every segment or with naked segments	On every segment or with naked segments	With naked segments	With naked segments	On every segment or with naked segments
Branches in trichoblast axils	No	Yes / No	Yes / No	No	Yes / No	No

Trichoblast cell nuclei and pigmentation	Uninucleate; Pigmentation absent	Multinucleate; Pigmentation absent (Present)	Uninucleate; Pigmentation absent	Trichoblasts absent	Uninucleate; Pigmentation absent	Uninucleate; Pigmentation absent
Branching pattern	Spiral, pseudodichotomous	Spiral, pseudodichotomous, dorsiventral	Pseudodichotomous	Dorsiventral, spiral, pseudodichotomous	Spiral, pseudodichotomous	Dorsiventral, spiral, pseudodichotomous
Spermatangial branches	Replacing trichoblasts (or on a trichoblast branch in <i>P. devoniensis</i> and <i>P. kapraunii</i> ), with or without sterile apical cells	On a branch of trichoblasts (replacing them in <i>V. lanosa</i> ), with/without sterile apical cells	On a branch of trichoblasts, with sterile apical cells	Replacing trichoblasts, without sterile apical cells	On a branch of trichoblasts, with/without sterile apical cells	On a branch of trichoblasts, with/without sterile apical cells
Carpogonial branch	4-celled	4-celled	4-celled	Unknown	4-celled	3-celled
Cystocarp morphology	Globular; ovoid; urceolate	Globular; ovoid	Ovoid	Ovoid	Globular	Globular; ovoid
Cells of the ostiole	Similar to the cells	Similar to the cells	Similar to the cells	Larger than cells	Similar to the cells	(Similar to) Larger

	below	below	below	below	below	than cells below
Tetrasporangial rows	Straight (slightly spiral)	Straight or spiral (two per segment in <i>Ctenosiphonia</i> )	Straight or spiral	Straight or spiral	Straight or spiral	(Straight) Spiral
References	This work, 5, 6, 9, 15, 16, 18, 22.	This work, 1, 2, 3, 6, 7, 8; 16, 18, 20, 21, 24.	This work, 16, 21.	This work, 2, 3.	This work, 7, 13, 18, 22.	This work, 2, 3, 4, 6, 9, 10, 11, 12, 14, 16, 17, 18, 19, 20, 21, 22, 23, 24, 25.

References: <sup>1</sup>Abbott & Hollenberg (1976); <sup>2</sup>Adams (1991); <sup>3</sup>Adams (1994); <sup>4</sup>Bustamante *et al.* (2013 *b*); <sup>5</sup>Dawes & Mathieson (2008); <sup>6</sup>Díaz-Tapia & Bárbara (2013); <sup>7</sup>Díaz-Tapia *et al.* (2013*a*); <sup>8</sup>Díaz-Tapia *et al.* (2013*b*); <sup>9</sup>Hollenberg (1942); <sup>10</sup>Hollenberg (1968*a*); <sup>11</sup>Hollenberg & Norris (1977); <sup>12</sup>Kim & Lee (1999); <sup>13</sup>Kim & Kim (2014); <sup>14</sup>Kim & Kim (2016); <sup>15</sup>Kim *et al.* (1994); <sup>16</sup>Maggs & Hommersand (1993); <sup>17</sup>Mamoozadeh & Freshwater (2011); <sup>18</sup>Mamoozadeh & Freshwater (2012); <sup>19</sup>Muangmai *et al.* (2014); <sup>20</sup>Segi (1949); <sup>21</sup>Stegenga *et al.* (1997); <sup>22</sup>Stuercke & Freshwater (2010); <sup>23</sup>Uwai & Masuda (1999); <sup>24</sup>Womersley (2003); <sup>25</sup>Yoon (1986).

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Table 2. Genus *Vertebrata* with new combinations resulting from the present study

Binomial in <i>Vertebrata</i> Basionym Synonyms	Type material Type locality
<i>Vertebrata constricta</i> (Womersley) Díaz-Tapia & Maggs, comb. nov. <i>Polysiphonia constricta</i> Womersley (1979, 497-498; Southern Australian species of <i>Polysiphonia</i> Greville (Rhodophyta). <i>Australian Journal of Botany</i> , <b>27</b> : 459-528)	Holotype: AD A32927 Kangaroo I., South Australia; 21.xi.1968
<i>Vertebrata foetidissima</i> (Cocks ex Bornet) Díaz-Tapia & Maggs, comb. nov. <i>Polysiphonia foetidissima</i> Cocks ex Bornet (1892, pp. 314-315; Les algues de P. K. A. Schousboe..... <i>Mémoires de la Société Nationale des Sciences naturelles et Mathématiques de Cherbourg</i> , <b>28</b> : 165-376.)	Lectotype (Maggs & Hommersand, 1993): PC 0146017 Plymouth, England; undated
<i>Vertebrata isogona</i> (Harvey) Díaz-Tapia & Maggs, comb. nov. <i>Polysiphonia isogona</i> Harvey (in Hooker 1855, p. 231; <i>The botany of the Antarctic voyage</i> .... Reeve, London.)	Lectotype (Womersley, 1979): BM 1082304 Blind Bay, Cook's Straits, New Zealand; viii.1849

<p><i>Vertebrata lobophoralis</i> (N.R.Mamoozadeh &amp; D.W.Freshwater) D.W.Freshwater</p> <p><i>Polysiphonia lobophoralis</i> N.R.Mamoozadeh &amp; D.W.Freshwater (2012, pp. 331-333; <i>Polysiphonia sensu lato</i> (Ceramiales, Florideophyceae) species of Caribbean Panama including <i>Polysiphonia lobophoralis</i> sp. nov. and <i>Polysiphonia nuda</i> sp. nov. <i>Botanica Marina</i>, <b>55</b>: 317–347.)</p>	<p>Holotype: US 217938</p> <p>Bocas del Toro, Panama;</p> <p>6.viii.2010</p>
<p><i>Vertebrata nigra</i> (Hudson) Díaz-Tapia &amp; Maggs, comb. nov.</p> <p><i>Conferva nigra</i> Hudson (1762, p. 481; <i>Flora anglica.... Prostant venales apud J. Nourse in the Strand &amp; C. Moran in Covent-Garden, London.</i>)</p> <p><i>Polysiphonia nigra</i> (Hudson) Batters</p>	<p>Neotype (Maggs &amp; Hommersand, 1993): BM 1067621</p> <p>Marsden, Durham, England;</p> <p>12.vi.1971</p>
<p><i>Vertebrata reptabunda</i> (Suhr) Díaz-Tapia &amp; Maggs, comb. nov.</p> <p><i>Hutchinsia reptabunda</i> Suhr (1831, p. 684; Beschreibung einiger neuen Algen. <i>Flora</i> 14: 673-687, 709-716, 725-731)</p> <p><i>Lophosiphonia reptabunda</i> (Suhr) Kylin</p>	<p>Holotype: L 955.62.97</p> <p>Biarritz, Pyrénées-Atlantiques, France</p>

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Table 3. Genus *Vertebrata* with resurrected names resulting from the present study.

Binomial in <i>Vertebrata</i> Basionym Synonyms	Type material Type locality
<i>Vertebrata aterrima</i> (J.D.Hooker & Harvey) Kuntze <i>Polysiphonia aterrima</i> J.D.Hooker & Harvey	Probable syntypes: TCD 12786-8, BM 1067593-6 and BM 1067598 New Zealand
<i>Vertebrata australis</i> (C.Agardh) Kuntze <i>Cladostephus australe</i> C.Agardh <i>Brongniartella australis</i> (C.Agardh) F.Schmitz	Lectotype (Parsons, 1980): PC Western Australia
<i>Vertebrata byssoides</i> (Goodenough & Woodward) Kuntze <i>Fucus byssoides</i> Goodenough & Woodward <i>Brongniartella byssoides</i> (Goodenough & Woodward) F.Schmitz	Lectotype (Maggs & Hommersand, 1993): BM Christchurch, England; 1794
<i>Vertebrata fruticulosa</i> (Wulfen) Kuntze <i>Fucus fruticulosus</i> Wulfen	Lectotype (Maggs & Hommersand, 1993): Wulfen (1789), pl. 16, fig. 1

<i>Boergeseniella fruticulosa</i> (Wulfen) Kylin	Trieste [Tergestum], Adriatic
<i>Vertebrata fucooides</i> (Hudson) Kuntze	Neotype (Maggs & Hommersand,
<i>Conferva fucooides</i> Hudson	1993): BM 807101
<i>Polysiphonia fucooides</i> (Hudson) Greville	Unlocalized, undated
<i>Vertebrata furcellata</i> (C.Agardh) Kuntze	Lectotype (Maggs & Hommersand,
<i>Hutchinsia furcellata</i> C.Agardh	1993): LD 40907
<i>Polysiphonia furcellata</i> (C.Agardh) Harvey	Brittany, France; undated
<i>Vertebrata hypnoides</i> (Welwitsch) Kuntze	Holotype: LD Agardh's herbarium
<i>Polysiphonia hypnoides</i> Welwitsch ex J.Agardh	no. 39346
<i>Ctenosiphonia hypnoides</i> (Welwitsch ex J.Agardh) Falkenberg	Lisbon, Portugal
<i>Vertebrata lanosa</i> (Linnaeus) T.A.Christensen	Holotype: LINN 1274.23
<i>Fucus lanosus</i> Linnaeus	Iceland, undated
<i>Polysiphonia lanosa</i> (Linnaeus) Tandy	
<i>Vertebrata simulans</i> (Harvey) Kuntze	Lectotype (Maggs & Hommersand,
<i>Polysiphonia simulans</i> Harvey	1993): BM-K
	Devon, England; 20.v.1831
<i>Vertebrata stimpsonii</i> (Harvey) Kuntze	Holotype: TCD 11956



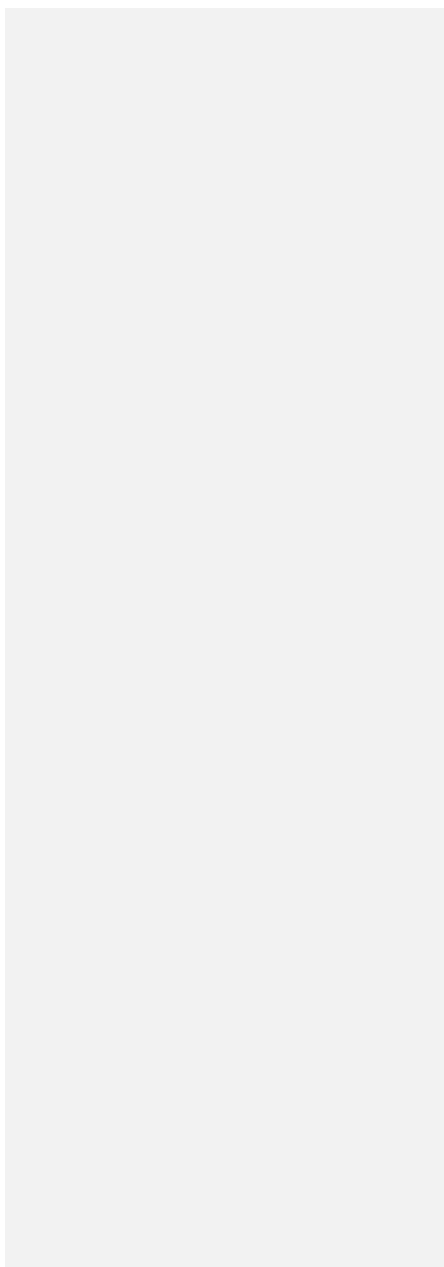
<i>Polysiphonia stimpsonii</i> Harvey	Hakodate Bay, Japan
<i>Enelittosiphonia stimpsonii</i> (Harvey) Kudo & Masuda	
<i>Vertebrata subulifera</i> (C.Agardh) Kuntze	Lectotype (Maggs & Hommersand, 1993): LD 41607
<i>Hutchinsia subulifera</i> C.Agardh	Venice, Italy; undated
<i>Polysiphonia subulifera</i> (C.Agardh) Harvey	
<i>Vertebrata thuyoides</i> (Harvey) Kuntze	Lectotype (Maggs & Hommersand, 1993): TCD
<i>Polysiphonia thuyoides</i> Harvey	Milltown Malbay, Ireland; 1831
<i>Boergeseniella thuyoides</i> (Harvey) Kylin	
<i>Vertebrata tripinnata</i> (J.Agardh) O.Kuntze	Lectotype (Diaz-Tapia <i>et al.</i> , 2013b): LD J. Agardh's Herbarium 40938
<i>Polysiphonia tripinnata</i> J.Agardh (1842, p. 142; <i>Algae maris Mediterranei et Adriatici</i> , observationes in diagnosin specierum et dispositionem generum. Apud Fortin, Masson et Cie, Paris.)	Trieste, Italy
[Kuntze transferred " <i>Polysiphonia tripinnata</i> Harvey" to <i>Vertebrata</i> , presumably a typographical error as the basionym is <i>P. tripinnata</i> J.Agardh (1842)]	
<i>Vertebrata urbana</i> (Harvey) Kuntze	Probable Holotype: TCD 186
<i>Polysiphonia urbana</i> Harvey	Table Bay, Cape Province, South Africa

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**Note:** The positions of *Polysiphonia paniculata* in the *rbcL* and 18S trees are not congruent. This suggests that these two sequences, generated from samples from Chile and California, respectively (Table S1), were obtained from different species. The assignment of this species to the genus *Vertebrata* therefore requires further study to clarify the identity of the two published sequences. The type locality is Peru.

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Table 4. Genus *Melanothamnus* with new combinations resulting from the present study.

New combination (if any) Basionym Synonyms	Type material Type locality, collection date	Notes
<i>Melanothamnus somalensis</i> Bornet & Falkenberg	Probable syntypes: PC 584990-2 Somalia	Figs 3-8
<i>Melanothamnus afaqhusainii</i> M.Shameel	Holotype: KUH-SW SAH-127 Pakistan	
<i>Melanothamnus unilateralis</i> (Levring) Diaz-Tapia & Maggs, comb. nov. <i>Fernandosiphonia unilateralis</i> Levring (1941, pp. 660-662; Die Meeresalgen der Juan Fernandez-Inseln. Die Corallinaceen der Juan Fernandez-Inseln. In: <i>The natural history of Juan Fernandez and Easter Island</i> (Skottsberg, C., editor) Vol. 2, 601-670; 753-757. Almqvist & Wiksells Boktryckeri,	Holotype: GB Juan Fernández Islands, Chile	Figs 9-18

Uppsala)		
<i>Melanothamnus apiculatus</i> (Hollenberg) Díaz-Tapia & Maggs, comb. nov. <i>Polysiphonia apiculata</i> Hollenberg (1968a, p. 61; An account of the species of <i>Polysiphonia</i> of the central and western tropical Pacific ocean. II <i>Oligosiphonia</i> . <i>Pacific Science</i> , 22: 56-98) <i>Neosiphonia apiculata</i> (Hollenberg) Masuda & Kogame	Holotype: US 48522  O'ahu Island, Hawai'i; 30.vii.1959	3-celled carpogonial branches (Kim & Abbott, 2006); plastid character  (Hollenberg 1968a; Fig. 9)
<i>Melanothamnus bajacali</i> (Hollenberg) Díaz-Tapia & Maggs, comb. nov. <i>Polysiphonia bajacali</i> Hollenberg (1961, pp. 347-348; Marine red algae of Pacific Mexico, Part 5: The genus <i>Polysiphonia</i> . <i>Pacific Naturalist</i> , 2: 345-375) <i>Neosiphonia bajacali</i> (Hollenberg) N.R.Mamoozadeh & D.W. Freshwater	Holotype: AHFH  Isla Guadalupe, Baja California, Mexico; 18.xii. 1949	"Cell walls hyaline" (Hollenberg, 1961).  Molecular data available from Yucatan, Mexico (Mamoozadeh & Freshwater, 2011)
<i>Melanothamnus balianus</i> (D.E.Bustamante, B.Y.Won & T.O.Cho) Díaz-Tapia & Maggs, com. nov. <i>Neosiphonia baliana</i> D.E.Bustamante, B.Y.Won & T.O.Cho	Holotype: CUK 7937  Blue Lagoon beach, Padang Bai, Karangasem, Bali, Indonesia; 27.iv.	Molecular data from the type locality  (Bustamante <i>et al.</i> , 2013b)

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(2013 <i>b</i> , pp. 516-518; <i>Neosiphonia baliana</i> sp. nov. and <i>N. silvae</i> sp. nov. (Rhodomelaceae, Rhodophyta) from Bali, Indonesia. <i>Botanica Marina</i> , <b>56</b> : 515-524)	2012.	
<i>Melanothamnus blandii</i> (Harvey) Díaz-Tapia & Maggs, comb. nov. <i>Polysiphonia blandii</i> Harvey (1862, pl. 184; <i>Phycologia australica</i> .... Vol. 4. Lovell Reeve & Co, London)	Lectotype (Womersley, 1979): TCD Brighton, Port Phillip, Victoria, Australia	3-celled carpogonial branches; plastid character. Molecular data available from the type locality (this work)
<i>Melanothamnus cheloniae</i> (Hollenberg & J.N.Norris) Díaz-Tapia & Maggs, comb. nov. <i>Polysiphonia sphaerocarpa</i> var. <i>cheloniae</i> Hollenberg & J.N.Norris (1977, p. 16-17; The red alga <i>Polysiphonia</i> (Rhodomelaceae) in the Northern Gulf of California. <i>Smithsonian Contributions to the Marine Sciences</i> , 1: 1-21.) <i>Neosiphonia cheloniae</i> (Hollenberg & J.N.Norris) J.N.Norris	Holotype: US 160602 Sonora, Gulf of California, Mexico; 21.i.1974	Plastid character (Hollenberg & Norris, 1977; fig. 4B)
<i>Melanothamnus collabens</i> (C.Agardh) Díaz-Tapia & Maggs, comb. nov. <i>Hutchinsia collabens</i> C.Agardh (1824, p. 153; <i>Systema algarum</i> .	Syntypes: LD Agardh herbarium 40885-40887 and 40890-40898; Cádiz, Spain	3-celled carpogonial branches; plastid character; molecular data available from the type locality (Díaz-Tapia & Bárbara,

<p>Berlinginiana, Lundae)</p> <p><i>Polysiphonia collabens</i> (C.Agardh) Kützing</p> <p><i>Streblocladia collabens</i> (C.Agardh) Falkenberg</p> <p><i>Neosiphonia collabens</i> (C.Agardh) Díaz-Tapia &amp; Bárbara</p>		2013)
<p><i>Melanothamnus concinnus</i> (Hollenberg) Díaz-Tapia &amp; Maggs, comb. nov.</p> <p><i>Polysiphonia concinna</i> Hollenberg (1944, pp. 474-475; An account of the species of <i>Polysiphonia</i> on the Pacific coast of North America. II. <i>Polysiphonia</i>. <i>American Journal of Botany</i>, 31: 474-483)</p> <p><i>Polysiphonia johnstonii</i> var. <i>concinna</i> (Hollenberg) Hollenberg</p> <p><i>Neosiphonia concinna</i> (Hollenberg) J.N.Norris</p>	<p>Holotype: US 61210; La Jolla, California, USA; 26.xii.1936.</p>	<p>Plastid character observed in our study of the type material</p>
<p><i>Melanothamnus decumbens</i> (T.Segi) Díaz-Tapia &amp; Maggs, comb. nov.</p> <p><i>Polysiphonia decumbens</i> T.Segi (1951, p. 218; Systematic study of the genus <i>Polysiphonia</i> from Japan and its vicinity. <i>Journal of the Faculty of Fisheries, Prefectural University of Mie</i>, 1:</p>	<p>Holotype: SAP 25880; Mihonoseki, Shimane Prefecture, Japan; vi.1948.</p>	<p>3-celled carpogonial branches; plastid character (Kim, 2003, fig. 5F). Molecular data available from Korea (Kim &amp; Yang, 2006)</p>

169-272) <i>Neosiphonia decumbens</i> (T.Segi) M.-S.Kim & I.K.Lee		
<i>Melanothamnus ecorticatus</i> (R.E.Norris) Díaz-Tapia & Maggs, comb. nov. <i>Fernandosiphonia ecorticata</i> R.E.Norris (1994, p. 434; Some cumophytic Rhodomelaceae (Rhodophyta) occurring in Hawaiian surf. <i>Phycologia</i> 33: 434-443)	Holotype: BISH 630042 Keokea Bay, Hawai'i; v.1990	Plastid character; ostiolar cells larger than other pericarpial cells (Abbott, 1999)
<i>Melanothamnus eastwoodiae</i> (Setchell & N.L.Gardner) Díaz- Tapia & Maggs, comb. nov. <i>Polysiphonia eastwoodiae</i> Setchell & N.L.Gardner (1930, p. 161, as <i>P. eastwoodae</i> ; Marine algae of the Revillagigedo Islands expedition in 1925. <i>Proceedings of the California Academy of Sciences</i> , 4: 109-215) <i>Neosiphonia eastwoodae</i> (Setchell & N.L.Gardner) Xiang Si- duan	Holotype: CAS 173674 Islas Revillagigedo	Plastid character observed in type material
<i>Melanothamnus ferulaceus</i> (Suhr ex J.Agardh) Díaz-Tapia &	Type materials are in LD, J.Agardh's	Plastid character in Panama and Brazil.

<p>Maggs, comb. nov.</p> <p><i>Polysiphonia ferulacea</i> Suhr ex J.Agardh (1863, p. 980; <i>Species Genera et Ordines Algarum</i>..... C.W.K. Glerup, Lundae)</p> <p><i>Neosiphonia ferulacea</i> (Suhr ex J.Agardh) S.M.Guimarães &amp; M.T.Fujii</p>	<p>Herbarium (not seen)</p> <p>Atlantic Mexico; North America; Guadeloupe; Hawaiian Islands; Marquesas Islands; Australia</p>	<p>Molecular data from Panama (Mamoozadeh &amp; Freshwater, 2012; Guimarães <i>et al.</i>, 2004)</p>
<p><i>Melanothamnus fibrillosus</i> (Okamura) Díaz-Tapia &amp; Maggs, comb. nov.</p> <p><i>Pterosiphonia fibrillosa</i> Okamura (1912, p. 172; <i>Icones of Japanese Algae. Vol. II (10)</i>. Privately published, Tokyo)</p> <p><i>Kintarosiphonia fibrillosa</i> (Okamura) S. Uwai &amp; Masuda</p>	<p>Lectotype (Uwai &amp; Masuda, 1999): SAP</p> <p>Shirahama, Chiba Prefecture, Japan; undated</p>	<p>3-celled carpogonial branches, plastid character, cells surrounding the ostiole much larger than the cells below (Uwai &amp; Masuda, 1999, figs. 18, 19).</p>
<p><i>Melanothamnus flavimarinus</i> (M.-S.Kim &amp; I.K.Lee) Díaz-Tapia &amp; Maggs, comb. nov.</p> <p><i>Neosiphonia flavimarina</i> M.-S.Kim &amp; I.K.Lee (1999, p. 272; <i>Neosiphonia flavimarina</i> gen. et sp. nov. with a taxonomic reassessment of the genus <i>Polysiphonia</i> (Rhodomelaceae, Rhodophyta). <i>Phycological Research</i>, 47: 271-281)</p>	<p>Holotype: SNU IBA001</p> <p>Bangpo, Anmyondo, Korea; 17.vii.1988.</p>	<p>3-celled carpogonial branches; plastid character (Kim &amp; Lee, 1999, fig. 5). Molecular data available from the type locality (Kim &amp; Yang, 2006)</p>
<p><i>Melanothamnus forfex</i> (Harvey) Díaz-Tapia &amp; Maggs, comb.</p>	<p>Lectotype (Womersley, 1979): TCD</p>	<p>3-celled carpogonial branches; plastid</p>



<p>nov.</p> <p><i>Polysiphonia forfex</i> Harvey (1859, pl. XCVI; <i>Phycologia Australica</i>.... Vol. 2. Lovell Reeve &amp; Co, London)</p>	<p>15353-4</p> <p>Rottneest Island, Western Australia</p>	<p>character, molecular data available from the type locality (this work)</p>
<p>comb. nov.</p> <p><i>Polysiphonia gorgoniae</i> Harvey (1853, p. 39; <i>Nereis boreali-americana</i>.... <i>Smithsonian Contributions to Knowledge</i>, 5: [i-ii], [1]-258, pls XIII-XXXVI)</p> <p><i>Neosiphonia gorgoniae</i> (Harvey) S.M.Guimarães &amp; M.T.Fujii</p>	<p>Syntypes: TCD 12801-4, NY 900637-8</p> <p>Key West, Florida, U.S.A</p>	<p>3-celled carpogonial branches observed in Brazil (Guimaraes, <i>et al.</i>, 2004); plastid character observed in type material (this work)</p>
<p>nov.</p> <p><i>Polysiphonia harlandii</i> Harvey (1860, p. 330; <i>Characters of new algae</i>.... <i>Proceedings of the American Academy of Arts and Sciences</i>, 4: 327-335)</p> <p><i>Neosiphonia harlandii</i> (Harvey) M.S.Kim &amp; I.K.Lee</p>	<p>Probable syntypes: TCD 11955, US 56848</p> <p>Hong Kong</p>	<p>3-celled carpogonial branches. Molecular data available from Korea (Kim, 2003; Kim &amp; Yang, 2006)</p>
<p>nov.</p> <p><i>Melanothamnus harveyi</i> (Bailey) Díaz-Tapia &amp; Maggs, comb.</p>	<p>Lectotype (Maggs &amp; Hommersand, 1993): TCD 12810</p>	<p>3-celled carpogonial branches (this work); plastid character. Molecular data</p>

<p><i>Polysiphonia harveyi</i> Bailey (1848, p. 38; Continuation of the list of localities of algae in the United States. <i>Proceedings of the American Academy of Arts and Sciences</i>, 4: 327-335)</p> <p><i>Neosiphonia harveyi</i> (Bailey) M.-S.Kim, H.-G.Choi, Guiry &amp; G.W.Saunders</p>	<p>Bailey; Stonington, Connecticut, USA; vii.1847</p>	<p>available from the type locality (McIvor <i>et al.</i>, 2001)</p>
<p><i>Melanothamnus hawaiiensis</i> (Hollenberg) Díaz-Tapia &amp; Maggs, comb. nov.</p> <p><i>Polysiphonia hawaiiensis</i> Hollenberg (1968 <i>a</i>, pp. 66-67; An account of the species of <i>Polysiphonia</i> of the central and western tropical Pacific ocean. II <i>Oligosiphonia. Pacific Science</i>, 22: 56-98.)</p> <p><i>Neosiphonia hawaiiensis</i> (Hollenberg) M.-S.Kim &amp; I.A.Abbott</p>	<p>Holotype: US 48524 Waikiki beach, O'ahu Island, Hawai'i; 21.i.1963</p>	<p>3-celled carpogonial branches (Kim &amp; Abbott, 2006). Plastid character (Abbott, 1999, fig. 122C)</p>
<p><i>Melanothamnus incomptus</i> (Harvey) Díaz-Tapia &amp; Maggs, comb. nov.</p> <p><i>Polysiphonia incompta</i> Harvey (1847, p. 44; <i>Nereis australis</i>.... Reeve Brothers, London)</p>	<p>Probable holotype: TCD 192 False Bay, Cape Province, South Africa</p>	<p>Plastid character. Molecular data available from the type locality (this work)</p>
<p><i>Melanothamnus japonicus</i> (Harvey) Díaz-Tapia &amp; Maggs,</p>	<p>Lectotype (Masuda <i>et al.</i>, 1995):</p>	<p>Plastid character (this work); 3-celled</p>

<p>comb. nov.</p> <p><i>Polysiphonia japonica</i> Harvey (in M.C. Perry 1857, p. 331; <i>Account of the Botanical specimens.</i> (Gray, A., editor) <i>Narrative of the expedition of an American squadron to the China Seas and Japan....</i> Senate of the Thirty-third Congress, Second Session, Executive Document. House of Representatives, Washington)</p> <p><i>Neosiphonia japonica</i> (Harvey) M.S.Kim &amp; I.K.Lee</p>	<p>TCD 11905</p> <p>Hakodate, Japan; v.1854</p>	<p>carpogonial branches. Molecular data available from the type locality (Kim &amp; Yang, 2006)</p>
<p><i>Melanothamnus johnstonii</i> (Setchell &amp; Gardner) Díaz-Tapia &amp; Maggs, comb. nov.</p> <p><i>Polysiphonia johnstonii</i> Setchell &amp; Gardner (1924, p. 767; XXIX Expedition of the California Academy of Sciences to the Gulf of California in 1921. <i>The Marine Algae. Proceeding of the California Academy of Science, Series 4</i> 12: 695-949)</p> <p><i>Neosiphonia johnstonii</i> (Setchell &amp; N.L.Gardner) J.N.Norris</p>	<p>Holotype: CAS1361</p> <p>San Esteban Island, Gulf of California; iv.1921</p>	<p>Plastid character. Molecular data available from the type locality (this work).</p> <p>The sequence from California (KX756670) is only 0.1-0.2 % divergent in its <i>rbcL</i> sequence from <i>M. collabens</i> from Spain. Further studies are needed to clarify the possible synonymy between these two species that share the unusual</p>

		character of having (5-) 6 pericentral cells.
<i>Melanothamnus nudus</i> (N.R.Mamoozadeh & D.W.Freshwater) D.W.Freshwater <i>Polysiphonia nuda</i> N.R.Mamoozadeh & D.W.Freshwater (2012, p. 335; <i>Polysiphonia sensu lato</i> (Ceramiales, Florideophyceae) species of Caribbean Panama including <i>Polysiphonia lobophoralis</i> sp. nov. and <i>Polysiphonia nuda</i> sp. nov. <i>Botanica Marina</i> , 55: 317–347)	Holotype: US 211334 Parque de Juventud, Calle Primero, Colon, Caribbean coast of Panama; 20.v.2009	Molecular data available from the type locality (Mamoozadeh & Freshwater, 2012)
<i>Melanothamnus peruviansis</i> (D.E.Bustamante, B.Y.Won, M.E.Ramirez & T.O.Cho) Díaz-Tapia & Maggs, comb. nov. <i>Neosiphonia peruviansis</i> D.E.Bustamante, B.Y.Won, M.E.Ramirez & T.O.Cho (2012, p. 360; <i>Neosiphonia peruviansis</i> sp. nov. (Rhodomelacea, Rhodophyta) from the Pacific coast of South America. <i>Botanica Marina</i> , 55: 359-366)	Holotype: CUK 7976 Lagunillas, Pisco, Ica, southern coast of Lima, Peru; 21.viii.2008	Plastid character. Molecular data available from the type locality (Bustamante <i>et al.</i> , 2012, fig. 10)
<i>Melanothamnus platycarpus</i> (Børgesen) Díaz-Tapia & Maggs, comb. nov.	Probable syntypes: BM 1067681 and 106760	3-celled carpogonial branches; plastid character (Iyengar & Balakrishnan, 1949,

<p><i>Polysiphonia platycarpa</i> Børgesen (1934, p. 23; Some Indian Rhodophyceae especially from the shores of the Presidency of Bombay-IV. <i>Bulletin of Miscellaneous Information, Royal Botanic Gardens, Kew</i>, 1934: 1-30)</p>	<p>Bombay, India; 19.xii.1927</p>	<p>fig. 1)</p>
<p><i>Melanothamnus pseudovillum</i> (Hollenberg) Díaz-Tapia &amp; Maggs, comb. nov. <i>Polysiphonia pseudovillum</i> Hollenberg (1968 a, p. 73; An account of the species of <i>Polysiphonia</i> of the central and western tropical Pacific ocean. II <i>Oligosiphonia. Pacific Science</i>, 22: 56-98)</p>	<p>Holotype: US 61232; North Island, Johnston Islands; 22.vi.1965</p>	<p>Cell walls “hyaline” (Hollenberg, 1968 a). Molecular data available from Panama (Mamoozadeh &amp; Freshwater, 2011)</p>
<p><i>Melanothamnus ramireziae</i> (D.E.Bustamante, B.Y.Won &amp; T.O.Cho) Díaz-Tapia &amp; Maggs, comb. nov. <i>Neosiphonia ramirezii</i> D.E.Bustamante, B.Y.Won &amp; T.O.Cho (2013a, <i>Neosiphonia ramirezii</i> sp. nov. (Rhodomelaceae, Rhodophyta) from Peru. <i>Algae</i>, 28: 73-82.)</p>	<p>Holotype: CUK 6511 Lagunillas, Pisco, Ica, Peru; 21.viii.2008.</p>	<p>Plastid character, 3-celled carpogonial branches. Molecular data available from the type locality (Bustamante <i>et al.</i>, 2013a, fig. 1f)</p>
<p><i>Melanothamnus silvae</i> (D.E.Bustamante, B.Y.Won &amp; T.O.Cho) Díaz-Tapia &amp; Maggs, comb. nov.</p>	<p>Holotype: CUK 7976 Geger, Nusadua, Bali, Indonesia;</p>	<p>Plastid character. Molecular data available from the type locality</p>

<p><i>Neosiphonia silvae</i> D.E.Bustamante, B.Y.Won &amp; T.O.Cho (2013b, pp. 518-520; <i>Neosiphonia baliana</i> sp. nov. and <i>N. silvae</i> sp. nov. (Rhodomelaceae, Rhodophyta) from Bali, Indonesia. <i>Botanica Marina</i>, 56: 515-524)</p>	<p>26.iv.2012</p>	<p>(Bustamante <i>et al.</i>, 2013b, figs 22-23)</p>
<p><i>Melanothamnus simplex</i> (Hollenberg) Díaz-Tapia &amp; Maggs, comb. nov. <i>Polysiphonia simplex</i> Hollenberg, (1942, p. 782; An account of the species of <i>Polysiphonia</i> on the Pacific coast of North America. I. Oligosiphonia. <i>American Journal of Botany</i>, 29: 772-785) <i>Neosiphonia simplex</i> (Hollenberg) Y.-P.Lee</p>	<p>Holotype: US 61238 Laguna Beach, Orange County, California, U.S.A; 14.v.1937</p>	<p>Plastid character. Molecular data available from the type locality (this work). <i>RbcL</i> sequence not included in our phylogeny because it is only 1% divergent from <i>N. ramirezii</i>.</p>
<p><i>Melanothamnus sphaerocarpus</i> (Børgesen) Díaz-Tapia &amp; Maggs, comb. nov. <i>Polysiphonia sphaerocarpa</i> Børgesen (1918, p. 271; The marine algae of the Danish West Indies. Part 3. Rhodophyceae (4). <i>Dansk Botanisk Arkiv</i>, 3: 241-304.) <i>Neosiphonia sphaerocarpa</i> (Børgesen) M.-S.Kim &amp; I.K.Lee</p>	<p>Isotypes: US , C Store Nordsidebugt, St. Thomas, Virgin Islands</p>	<p>Plastid character. Molecular data available from Florida (Mamoozadeh &amp; Freshwater, 2011, fig. 18)</p>

<p><i>Melanothamnus strictissimus</i> (J.D.Hooker &amp; Harvey) Díaz-Tapia &amp; Maggs, comb. nov.</p> <p><i>Polysiphonia strictissima</i> J.D.Hooker &amp; Harvey (1845, p. 538; Algae Novae Zelandiae.... <i>London Journal of Botany</i>, 4: 521-551.)</p>	<p>Probable syntype: BM 561312</p> <p>New Zealand</p>	<p>Plastid character (this work). Molecular data available from the type locality (Stuercke &amp; Freshwater, 2010)</p>
<p><i>Melanothamnus thailandicus</i> (N.Muangmai &amp; C.Kaewsuralikhit) Díaz-Tapia &amp; Maggs, comb. nov.</p> <p><i>Neosiphonia thailandica</i> N.Muangmai &amp; C.Kaewsuralikhit (2014, pp. 460-461; The new species <i>Neosiphonia thailandica</i> sp. nov. (Rhodomelaceae, Rhodophyta) from the Gulf of Thailand. <i>Botanica Marina</i>, 57: 459-467)</p>	<p>Holotype: KUMF-SRC 03-011-1</p> <p>Sri Racha Harbor, Chon Buri, Thailand; 11.iii.2011</p>	<p>3-celled carpogonial branches. Molecular data available from the type locality (Muangmai <i>et al.</i>, 2014)</p>
<p><i>Melanothamnus yongpilii</i> (B.Kim &amp; M.-S.Kim) Díaz-Tapia &amp; Maggs, comb. nov.</p> <p><i>Neosiphonia yongpilii</i> B.Kim &amp; M.-S.Kim (2016, pp. 324-325; <i>Neosiphonia yongpilii</i> sp. nov. (Rhodomelaceae, Rhodophyta), known as <i>Neosiphonia simplex</i> from Korea, with an emphasis on cystocarp development. <i>Phycologia</i>, 55: 323-332)</p>	<p>Holotype: JNUB 140704-101</p> <p>Jongdal, Jeju Island, Korea; 04.iv.2014</p>	<p>3-celled carpogonial branches; plastid character. Molecular data available from the type locality (Kim &amp; Kim, 2016, fig. 14)</p>

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Note: Here we include only species that we can confidently assign to this genus (i.e., we have examined type material or suitable pictures of the type material showing the plastid character and/or sequences are available from the type locality or nearby).

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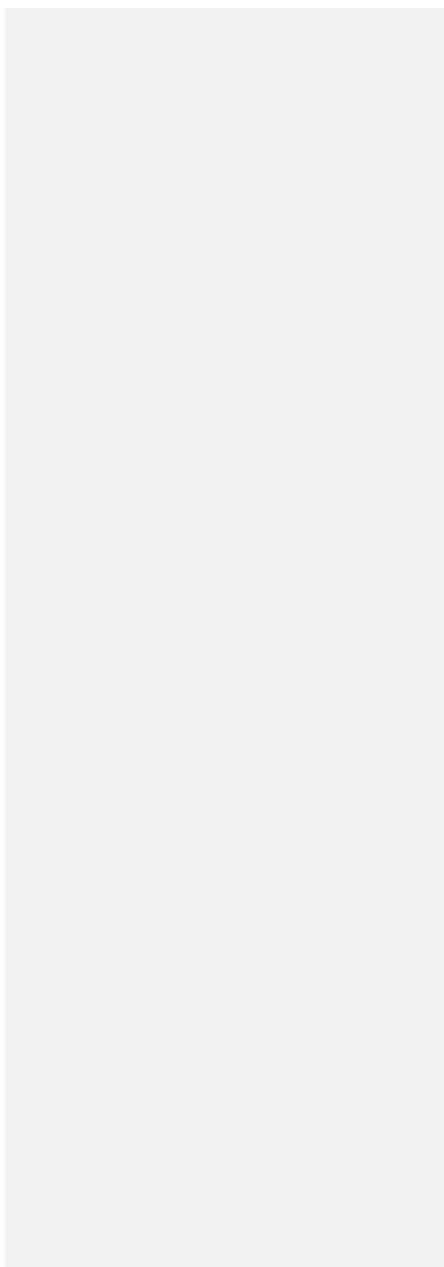




Table 5. New combinations in *Melanothamnus* made for formal reasons (because the current genus is here placed in synonymy with *Melanothamnus*) although type material has not been examined

Binomial in <i>Melanothamnus</i> (if any) Basionym Synonyms	Type material Type locality	Notes
<i>Melanothamnus hancockii</i> (Dawson) Díaz-Tapia & Maggs, comb. nov. <i>Polysiphonia hancockii</i> E.Y.Dawson (1944, pp. 331-332; The marine algae of the Gulf of California. Allan Hancock Pacific Expeditions 3: 189-432) <i>Fernandosiphonia hancockii</i> (Dawson) R.E.Norris	Holotype: LAM EYD629c Baja California, Mexico; 16.ii.1940	Plastid character. Molecular data from Japan (this work)
<i>Melanothamnus masonii</i> (Setchell & N.L.Gardner) Díaz-Tapia & Maggs, comb. nov.	Holotype: CAS 173618 Isla Guadalupe, México; iv.1925	

<p><i>Polysiphonia masonii</i> Setchell &amp; Gardner (1930, p. 160; Marine algae of the Revillagigedo Islands expedition in 1925. <i>Proceedings of the California Academy of Sciences</i>, 4: 109-215)</p> <p><i>Neosiphonia masonii</i> (Setchell &amp; N.L.Gardner) J.N.Norris</p>		
<p><i>Melanothamnus minutissimus</i> (Hollenberg) Díaz-Tapia &amp; Maggs, comb. nov.</p> <p><i>Polysiphonia minutissima</i> Hollenberg (1942, p. 781, An account of the species of <i>Polysiphonia</i> on the Pacific coast of North America. I. Oligosiphonia. <i>American Journal of Botany</i>, 29: 772-785)</p>	<p>Holotype: US 66797 Punta Banda, Baja California, Mexico; 17.xii.1938</p>	<p>Plastid character. Molecular data from Japan (this work)</p>
<p><i>Melanothamnus nanus</i> (A.J.K.Millar) Díaz-Tapia &amp; Maggs, comb. nov</p> <p><i>Fernandosiphonia nana</i> A.J.K.Millar (1990, p. 439; Marine red algae of the Coffs Harbour region, northern New South Wales. <i>Australian Systematic Botany</i>, 3: 293-593)</p>	<p>Holotype: MELU AM752 Coffs Harbour, New South Wales; 27.viii.1980</p>	
<p><i>Melanothamnus notoensis</i> (Segi) Díaz-Tapia &amp; Maggs, comb.</p>	<p>Holotype: SAP 025894</p>	<p>Plastid character in Korea (Nam &amp; Kang,</p>

<p>nov.</p> <p><i>Polysiphonia notoensis</i> Segi (1951, p. 266; Systematic study of the genus <i>Polysiphonia</i> from Japan and its vicinity. <i>Journal of the Faculty of Fisheries, Prefectural University of Mie</i>, 1: 169-272)</p> <p><i>Neosiphonia notoensis</i> (Segi) M.S.Kim &amp; I.K.Lee</p>	<p>Shibagaki, Ishikawa Prefecture, Japan; 9.vii.1947</p>	<p>2012; fig. 47E)</p>
<p>comb. nov.</p> <p><i>Polysiphonia polyphysa</i> Kützing (1863, p. 20; <i>Tabulae phycologicae; oder, Abbildungen der Tange. Vol. XIII.</i> Gedruckt auf kosten des Verfassers (in commission bei W. Köhne), Nordhausen)</p> <p><i>Neosiphonia polyphysa</i> (Kützing) Skelton &amp; G.R.South</p>	<p>Holotype: L 4082747 Vieillard; New Caledonia; undated</p>	
<p>nov.</p> <p><i>Polysiphonia porrecta</i> Segi (1951, p. 260; Systematic study of the genus <i>Polysiphonia</i> from Japan and its vicinity. <i>Journal of the</i></p>	<p>Holotype: SAP 025867 Henashi, Nishitsugaru-gun, Aomori Prefecture, Japan; 19.vi.1948.</p>	<p>Plastid character in Korea (Lee, 2008; p. 314, fig. C)</p>

<p><i>Faculty of Fisheries, Prefectural University of Mie</i>, 1: 169-272)</p> <p><i>Neosiphonia porrecta</i> (Segi) Y.-P. Lee</p>		
<p><i>Melanothamnus savatieri</i> (Hariot) Díaz-Tapia &amp; Maggs, comb. nov.</p> <p><i>Polysiphonia savatieri</i> Hariot (1891, p. 226; Liste des algues marines rapportés de Yokoska (Japon) par M. le Dr Savatier. <i>Mémoires de la Société nationale des sciences naturelles de Cherbourg</i>, 27: 211-230)</p> <p><i>Neosiphonia savatieri</i> (Hariot) M.S.Kim &amp; I.K.Lee</p>	<p>Lectotype (Kim, 2005): PC 0011879</p> <p>Yokosuka, Kanagawa Prefecture, Japan</p>	<p>3-celled carpogonial branches in Malaysia (Masuda <i>et al.</i>, 2001).</p> <p>Molecular data available from Korea (Phillips <i>et al.</i>, 2000)</p>
<p><i>Melanothamnus sparsus</i> (Setchell) Díaz-Tapia &amp; Maggs, comb. nov.</p> <p><i>Lophosiphonia sparsa</i> Setchell (1926, p. 103; Tahitian algae collected by W.A. Setchell, C.B. Setchell and H.E. Parks. <i>University of California Publications in Botany</i>, 12: 61-142)</p> <p><i>Polysiphonia sparsa</i> (Setchell) Hollenberg</p> <p><i>Neosiphonia sparsa</i> (Setchell) I.A.Abbott</p>	<p>Holotype: UC 261144; Arue Reef, Tahiti; 27.vi.1922</p>	<p>Plastid character in Vietnam (Abbott <i>et al.</i>, 2002; fig. 27)</p>
<p><i>Melanothamnus teradomariensis</i> (M.Noda) Díaz-Tapia &amp; Maggs,</p>	<p>Holotype: Herbarium Niigata</p>	<p>Molecular data available from Korea</p>

<p>comb. nov.</p> <p><i>Polysiphonia teradomariensis</i> M.Noda (in Noda, M. &amp; Kitami, T. 1971, 47; Some species of marine algae from Echigo Province facing the Japan Sea. <i>Scientific Reports Niigata University, Ser. D. (Biology)</i>, 8: 35-52)</p> <p><i>Polysiphonia japonica</i> var. <i>teradomariensis</i> (M.Noda) H.Y.Yoon</p> <p><i>Neosiphonia teradomariensis</i> (M.Noda) M.-S.Kim &amp; I.K.Lee</p>	<p>University</p> <p>Echigo Province, Japan; 28.xi.1968</p>	<p>(Bárbara <i>et al.</i>, 2013)</p>
<p><i>Melanothamnus tongatensis</i> (Harvey ex Kützing) Díaz-Tapia &amp; Maggs, comb. nov.</p> <p><i>Polysiphonia tongatensis</i> Harvey ex Kützing, (1864, p. 14; <i>Tabulae phycologicae; oder, Abbildungen der Tange. Vol. XIV.</i> Gedruckt auf kosten des Verfassers (in commission bei W. Köhne), Nordhausen)</p> <p><i>Neosiphonia tongatensis</i> (Harvey ex Kützing) M.-S.Kim &amp; I.K.Lee</p>	<p>Holotype: L 4083619</p> <p>Tonga, Friendly Islands; undated</p>	<p>Molecular data available from Panama</p> <p>(Mamoozadeh &amp; Freshwater, 2011)</p>
<p><i>Melanothamnus upolensis</i> (Grunow) Díaz-Tapia &amp; Maggs, comb. nov.</p>	<p>Syntypes: W</p> <p>Upolu, Western Samoa</p>	<p>Molecular data available from Hawaii</p> <p>(Sherwood <i>et al.</i>, 2010)</p>

<p><i>Polysiphonia upolensis</i> Grunow (1874, p. 49; Algen der Fidschi-, Tonga- und Samoa-Inseln, gesammelt von Dr. E. Graeffe. <i>Journal des Museum Godeffroy</i>, 3: 23-50)</p> <p><i>Neosiphonia upolensis</i> (Grunow) M.S.Kim &amp; Boo</p>		
<p><i>Melanothamnus yendoii</i> (T.Segi) Díaz-Tapia &amp; Maggs, comb. nov.</p> <p><i>Polysiphonia yendoii</i> Segi (1951, p. 211; Systematic study of the genus <i>Polysiphonia</i> from Japan and its vicinity. <i>Journal of the Faculty of Fisheries, Prefectural University of Mie</i>, 1: 169-272)</p> <p><i>Neosiphonia yendoii</i> (Segi) M.-S.Kim &amp; I.K.Lee</p>	<p>Holotype: SAP 0258883</p> <p>Muroran, Hokkaido, Japan; 30.iv.1935</p>	<p>Molecular data available from Korea (Bárbara <i>et al.</i>, 2013)</p>
<p><i>Neosiphonia saccorhiza</i> (F.S.Collins &amp; Hervey) J.M.C.Nunes &amp; S.M.Guimarães, nom. inval.</p> <p><i>Lophosiphonia saccorhiza</i> F.S.Collins &amp; Hervey</p> <p><i>Polysiphonia saccorhiza</i> (F.S.Collins &amp; Hervey) Hollenberg</p>	<p>Isotypes: NY, Collins Herbarium</p> <p>Gibbet Island, Bermuda</p>	<p>Transfer to <i>Melanothamnus</i> is not made here as <i>N. saccorhiza</i> is an invalid combination (the basionym was not cited), and the phylogenetic affinities of <i>Lophosiphonia saccorhiza</i> are unknown.</p>

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Figure legends

**Fig. 1.** Phylogenetic tree estimated with ML analysis of *rbcL* sequences. Values at nodes indicate bootstrap support (BP)/posterior probability (PP) (only shown if > 60/0.6). Branches marked with an asterisk received 100% (BP)/1.00 (PP) support. Species names printed in bold correspond to type species of genera.

**Fig. 2.** Phylogenetic tree estimated with ML analysis of 18S sequences. Values at nodes indicate bootstrap support/posterior probability (only shown if > 60%/0.6 PP). Branches marked with an asterisk received 100%/1.00 PP support. Species names printed in bold correspond to type species of genera.

**Figs 3-8.** *Melanothamnus somalensis*, the type species of *Melanothamnus*. **Fig. 3.** Herbarium specimen MICH 662774. **Fig. 4.** Apical part of a specimen with alternately arranged branches. **Figs 5-6.** Apices of branches with (Fig. 5) or without (Fig. 6) abundant trichoblasts. **Fig. 7.** Apex of a lateral branch with trichoblasts. **Fig. 8.** Surface view of cells with the plastids lying exclusively on radial walls while the outer walls appear transparent (arrows). Scale bars: Fig. 3, 6 cm; Fig. 4, 1 mm; Figs 5 and 6, 350  $\mu\text{m}$ ; Fig. 7, 200  $\mu\text{m}$ ; Fig. 8, 100  $\mu\text{m}$ .

**Figs 9-18.** *Fernandosiphonia unilateralis* type material, the type species of *Fernandosiphonia*. **Fig. 9.** Herbarium specimen. **Figs 10-11.** Branches unilaterally arranged. **Fig. 12.** Axis with scar cells of trichoblasts (arrows). **Figs 13-14.** Surface view of pericentral cells with plastids lying only on the radial walls, so that the outer walls appear transparent (Fig. 13, arrows) and cells have a dark flank (Fig. 14). **Fig. 15.**

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Young spermatangial branch formed on the first dichotomy of a trichoblast, remaining the other vegetative branch (arrow). **Fig. 16.** Procarp (su = supporting cell; cp = carpogonium). **Fig. 17.** Cystocarp. **Fig. 18.** Tetrasporangia arranged in short spiral series. Scale bars: Fig. 9, 3 cm; Fig. 10, 2 mm; Fig. 11, 450  $\mu\text{m}$ ; Figs 12, 14, 17 and 18, 100  $\mu\text{m}$ ; Figs 13 and 15, 40  $\mu\text{m}$ ; Fig. 16, 20  $\mu\text{m}$ .

**Figs 19-24.** Rhizoid anatomy in the Polysiphonieae. In open connection with pericentral cells in *Polysiphonia stricta* (**Fig. 19**, *Polysiphonia sensu stricto* clade 1). Cut off from pericentral cells in *P. foetidissima* (**Fig. 20**, *Vertebrata* clade), *P. denudata* (**Fig. 21**, *Carradoriella* clade), *Polysiphonia* sp. (**Fig. 22**, *Streblocladia* clade), *P. schneideri* (**Fig. 23**, *P. schneideri* clade) and *P. incompta* (**Fig. 24**, *Melanothamnus* clade). Scale bars: Figs 19-23, 100  $\mu\text{m}$ ; Fig. 24, 500  $\mu\text{m}$ .

**Figs 25-39.** Plastid arrangement in the Polysiphonieae. Scattered against all cell walls of the pericentral cells in *Polysiphonia stricta* (**Figs 25-26**, *Polysiphonia sensu stricto* clade 1), *Vertebrata lanosa* (**Figs 27-28**, *Vertebrata* clade), *P. virgata* (**Figs 29-30**, *Carradoriella* clade), *Polysiphonia* sp. (**Fig. 31**, *Streblocladia* clade) and *P. schneideri* (**Figs 32-33**, *P. schneideri* clade). Lying exclusively on the radial walls of the pericentral cells in species of the *Melanothamnus* clade: *Neosiphonia collabens* (**Figs 34-35**), *N. harveyi* (**Figs 36-38**) and *P. forfex* (**Fig. 39**). Scale bars: Figs 25, 27, 29, 38 and 39, 500  $\mu\text{m}$ ; Figs 26, 28 and 30, 800  $\mu\text{m}$ ; Figs 31, 32, 34, 35 and 37, 100  $\mu\text{m}$ ; Fig. 33, 300  $\mu\text{m}$ ; Fig. 36, 50  $\mu\text{m}$ .

**Figs 40-46.** Trichoblast nuclei (arrows) in the Polysiphonieae. Uninucleate trichoblast cells in *Polysiphonia scopulorum* (**Fig. 40**, *Polysiphonia sensu stricto* clade 1), *P.*



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6 *denudata* (Fig. 44, *Carradoriella* clade), *P. schneideri* (Fig. 45, *P. schneideri* clade) and  
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8 *P. blandii* (Fig. 46, *Melanothamnus* clade). Multinucleate trichoblast cells in species of  
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10 the *Vertebrata* clade: *P. nigra* (Fig. 41), *Boergeseniella fruticulosa* (Fig. 42) and *P.*  
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12 *foetidissima* (Fig. 43). Scale bars: Figs 40-43, 60 µm, Fig. 44, 30 µm; Fig. 45, 20 µm;  
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14 Fig. 46, 100 µm.  
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18 **Figs 47-52.** Spermatangial branches in the Polysiphonieae. Replacing trichoblasts and  
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20 with sterile apical filaments in *Polysiphonia stricta* (Fig. 47, *Polysiphonia sensu stricto*  
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22 clade 1). Replacing trichoblasts and lacking sterile apical cells in *Vertebrata lanosa*  
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24 (Fig. 48, *Vertebrata* clade). On a branch of a trichoblast and with sterile apical cells in  
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26 *P. fucooides* (Fig. 49, *Vertebrata* clade), *P. denudata* (Fig. 50, *Carradoriella* clade), *P.*  
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28 *schneideri* (Fig. 51, *P. schneideri* clade) and *Neosiphonia harveyi* (Fig. 52,  
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30 *Melanothamnus* clade). Scale bars: 100 µm. Arrows show the apical sterile cells and  
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32 arrowheads the sterile branch of fertile trichoblasts.  
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36 **Figs 53-58.** Carpogonial branches in the Polysiphonieae. Four-celled in *Polysiphonia*  
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38 *stricta* (Fig. 53, *Polysiphonia sensu stricto* clade 1), *P. nigra* (Fig. 54, *Vertebrata*  
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40 clade), *P. denudata* (Fig. 55, *Carradoriella* clade) and *P. schneideri* (Fig. 56, *P.*  
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42 *schneideri* clade). Three-celled in species of the *Melanothamnus* clade: *Neosiphonia*  
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44 *harveyi* (Fig. 57) and *P. blandii* (Fig. 58). Su = supporting cell; st = sterile basal cell; 1-  
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46 4 cells of carpogonial branches. Scale bars: Fig. 53, 30 µm; Figs 54-58, 20 µm.  
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50 **Figs 59-64.** Cystocarps in the Polysiphonieae. Urceolate in *Polysiphonia stricta* (Fig.  
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52 59, *Polysiphonia sensu stricto* clade 1). Ovoid in *Vertebrata lanosa* (Fig. 60, *Vertebrata*  
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54 clade), *P. denudata* (Fig. 61, *Carradoriella* clade), *Streblocladia glomerulata* (Fig. 62,  
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*Streblocladia* clade). Globose in *Polysiphonia schneideri* (Fig. 63, *P. schneideri* clade) and *Neosiphonia collabens* (Fig. 64, *Melanothamnus* clade). Scale bars: Figs 59-62 and 64, 200 µm; Fig. 63, 100 µm.

**Figs 65-70.** Cells surrounding the ostiole in the Polysiphonieae. Similar or slightly larger than the cells of the pericarp immediately below in *Polysiphonia stricta* (Fig. 65, *Polysiphonia sensu stricto* clade 1), *Vertebrata lanosa* (Fig. 66, *Vertebrata* clade), *P. denudata* (Fig. 67, *Carradoriella* clade), and *P. schneideri* (Fig. 69, *P. schneideri* clade). They are much larger in *Streblocladia glomerulata* (Fig. 68, *Streblocladia* clade) and *Neosiphonia collabens* (Fig. 70, *Melanothamnus* clade). Scale bars: Figs 65-68 and 70, 100 µm; Fig. 69, 60 µm.

**Figs 71-76.** Tetrasporangia in the Polysiphonieae. Forming long straight series in *Polysiphonia stricta* (Fig. 71, *Polysiphonia sensu stricto* clade 1). Forming spiral series in *Vertebrata lanosa* (Fig. 72, *Vertebrata* clade), *Polysiphonia* sp. (Fig. 74, *Streblocladia* clade) and *Neosiphonia harveyi* (Fig. 76, *Melanothamnus* clade). Forming short straight series in *P. denudata* (Fig. 73, *Carradoriella* clade), and *P. schneideri* (Fig. 75, *P. schneideri* clade). Scale bars: Figs 71, 74 and 76, 200 µm; Figs 72, 73 and 75, 400 µm.

**Fig. 77.** World map representing the proportion of *Fernandosiphonia* (black) and other Polysiphonieae (grey) species in selected regions where the Polysiphonieae were studied in detail. Data were obtained from the following references after updating the species names: Alaska: Lindstrom (<http://www.seaweedsokalaska.com>); Brazil (Espírito Santo-São Paulo): Guimâraes *et al.* (2004); Hawaii: Abbott (1999); Japan: Yoshida

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6 (1998); Korea: Nam & Kang (2012); Panama: Mamoozadeh & Freshwater (2012);  
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8 Spain (Galicia): Bárbara *et al.* (2005); British Isles: Maggs & Hommersand (1993).  
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11 **Fig. S1.** Chronogram resulting from the Bayesian relaxed molecular clock analysis  
12 performed with BEAST.  
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15 **Fig. S2.** Chronogram resulting from the autocorrelated molecular clock analysis  
16 performed with PhyloBayes.  
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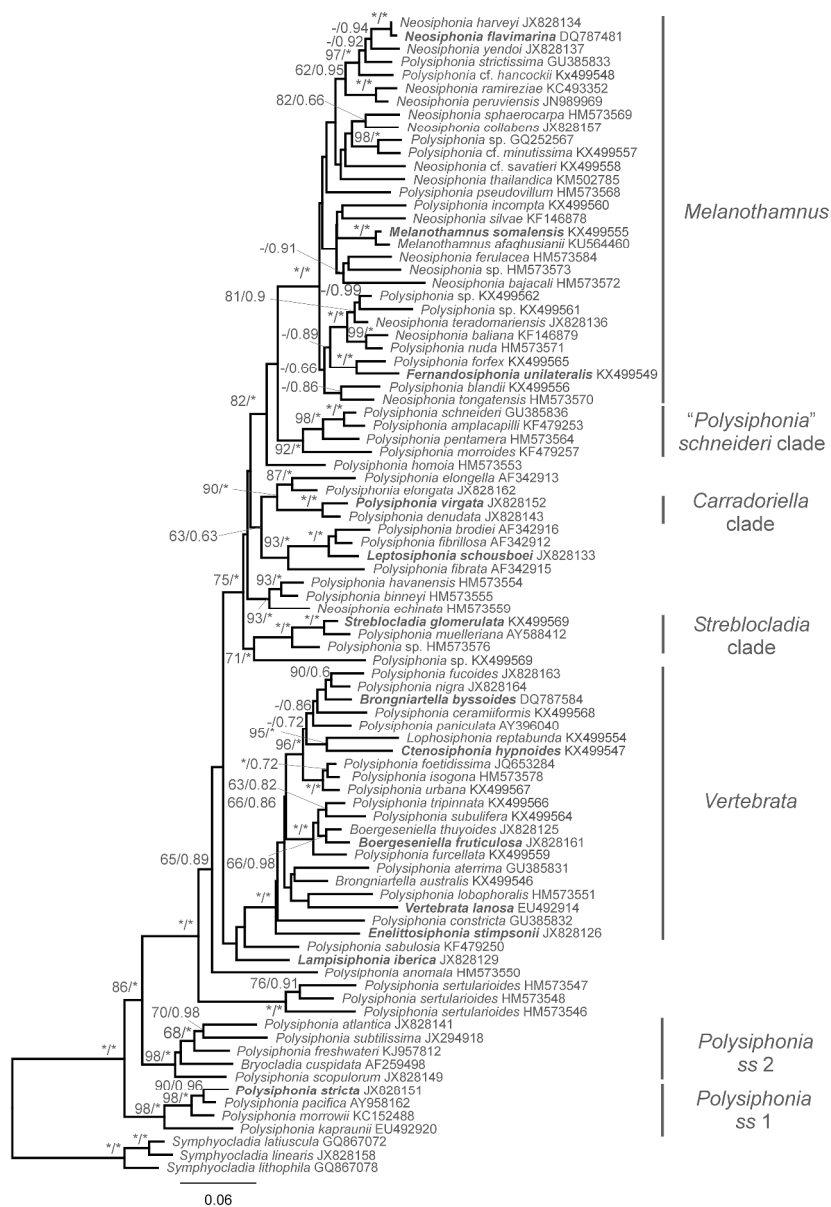


Fig. 1. Phylogenetic tree estimated with ML analysis of rbcL sequences. Values at nodes indicate bootstrap support (BP)/posterior probability (PP) (only shown if > 60/0.6). Branches marked with an asterisk received 100% (BP)/1.00 (PP) support. Species names printed in bold correspond to type species of genera.

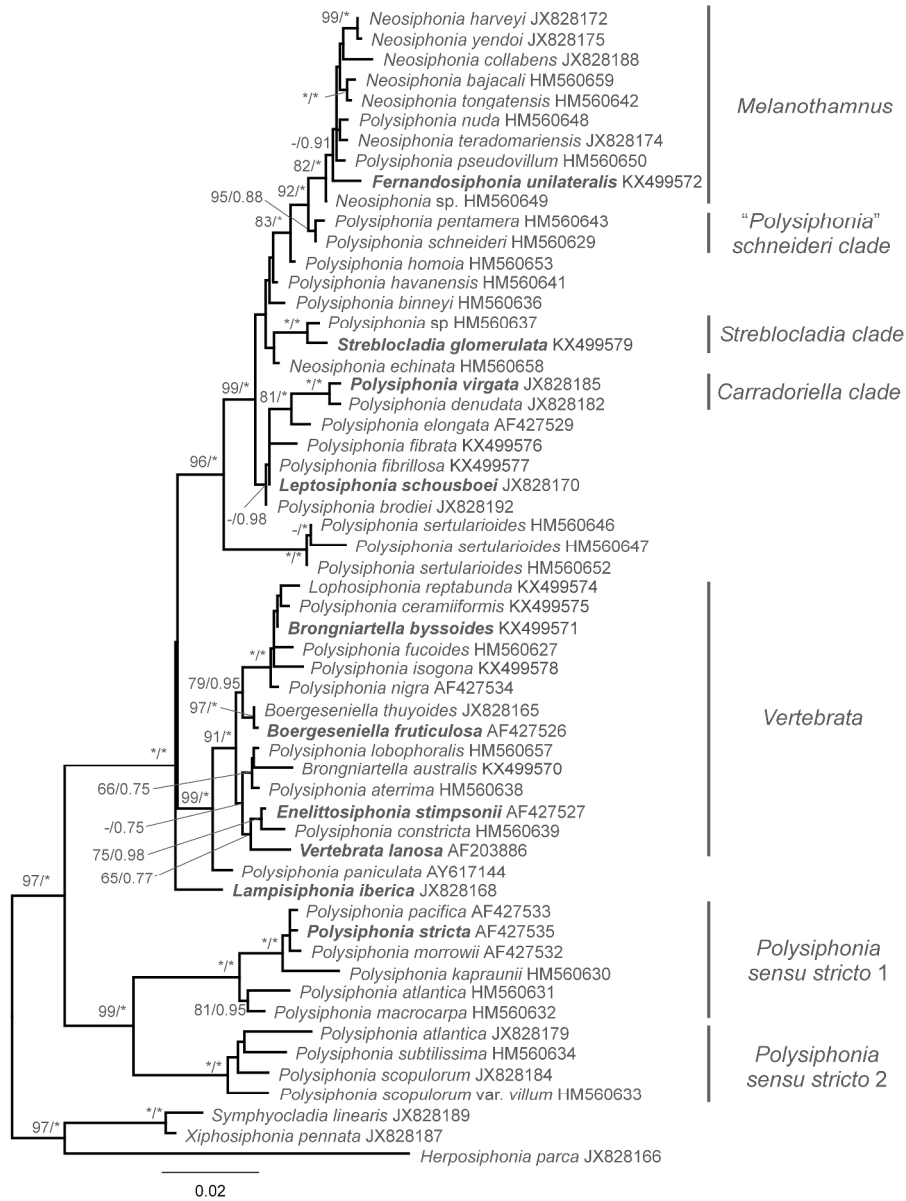
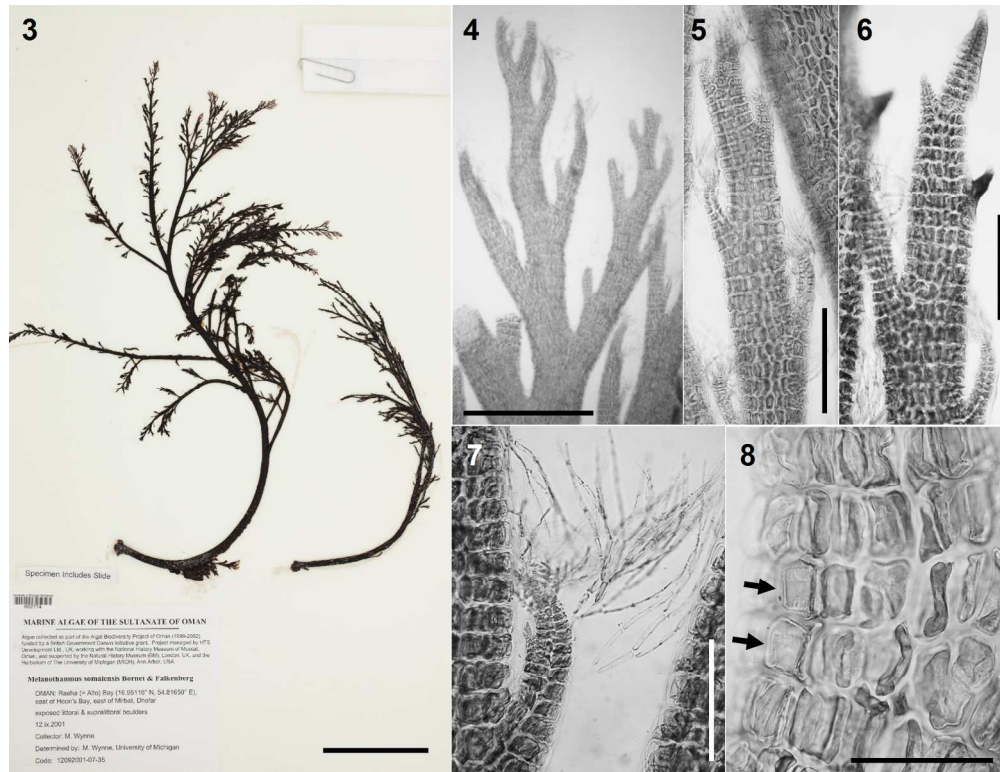
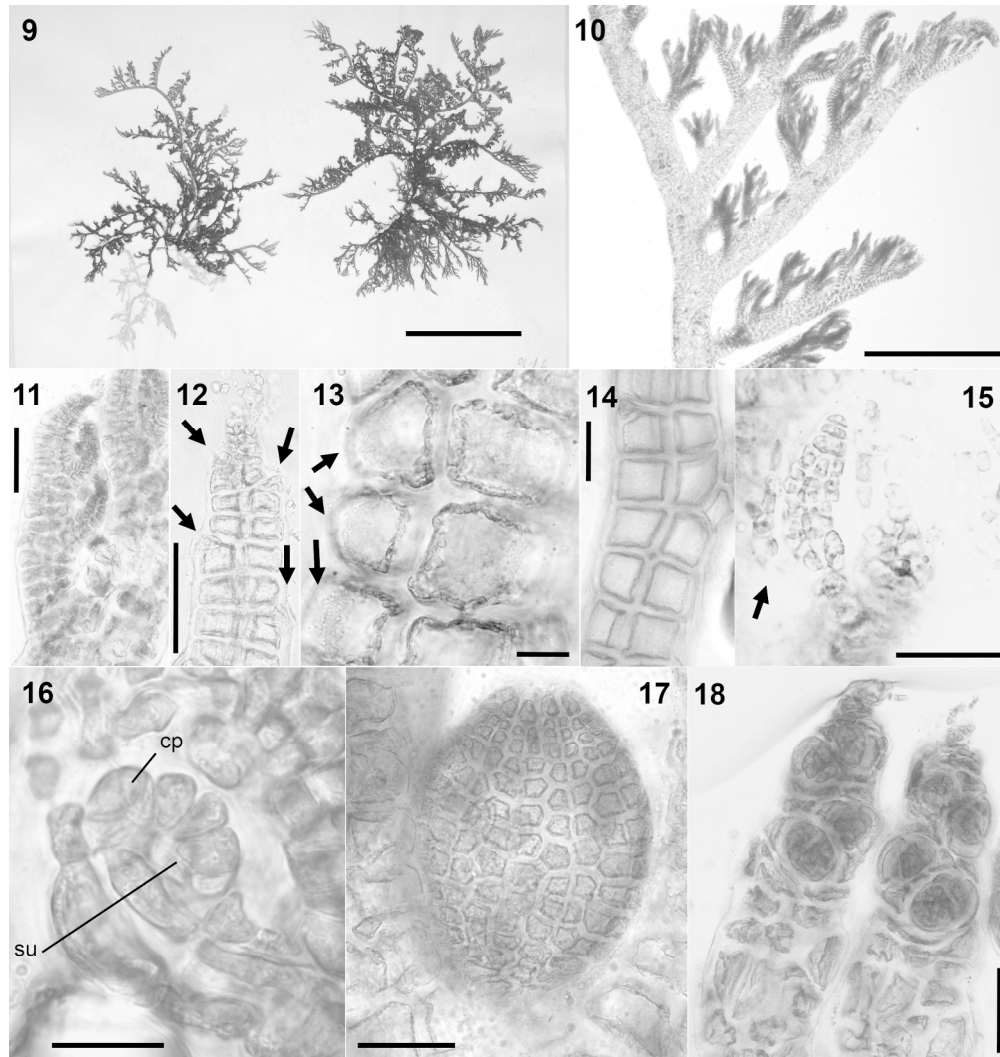


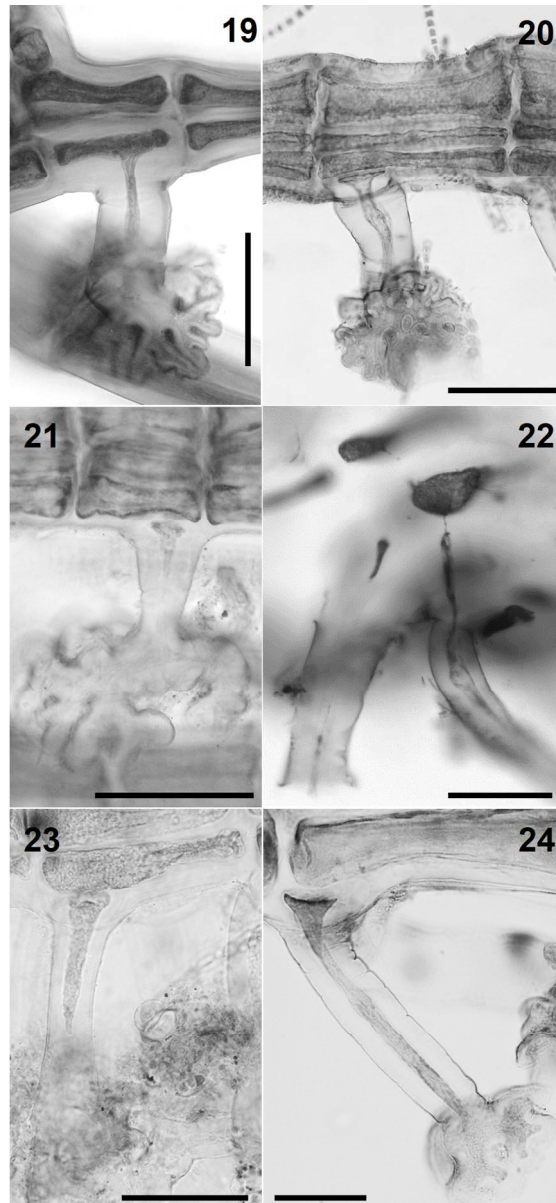
Fig. 2. Phylogenetic tree estimated with ML analysis of 18S sequences. Values at nodes indicate bootstrap support/posterior probability (only shown if > 60%/0.6 PP). Branches marked with an asterisk received 100%/1.00 PP support. Species names printed in bold correspond to type species of genera.



Figs 3-8. *Melanothamnus somalensis*, the type species of *Melanothamnus*. Fig. 3. Herbarium specimen MICH 662774. Fig. 4. Apical part of a specimen with alternately arranged branches. Figs 5-6. Apices of branches with (Fig. 5) or without (Fig. 6) abundant trichoblasts. Fig. 7. Apex of a lateral branch with trichoblasts. Fig. 8. Surface view of cells with the plastids lying exclusively on radial walls while the outer walls appear transparent (arrows). Scale bars: Fig. 3, 6 cm; Fig. 4, 1 mm; Figs 5 and 6, 350  $\mu\text{m}$ ; Fig. 7, 200  $\mu\text{m}$ ; Fig. 8, 100  $\mu\text{m}$ .

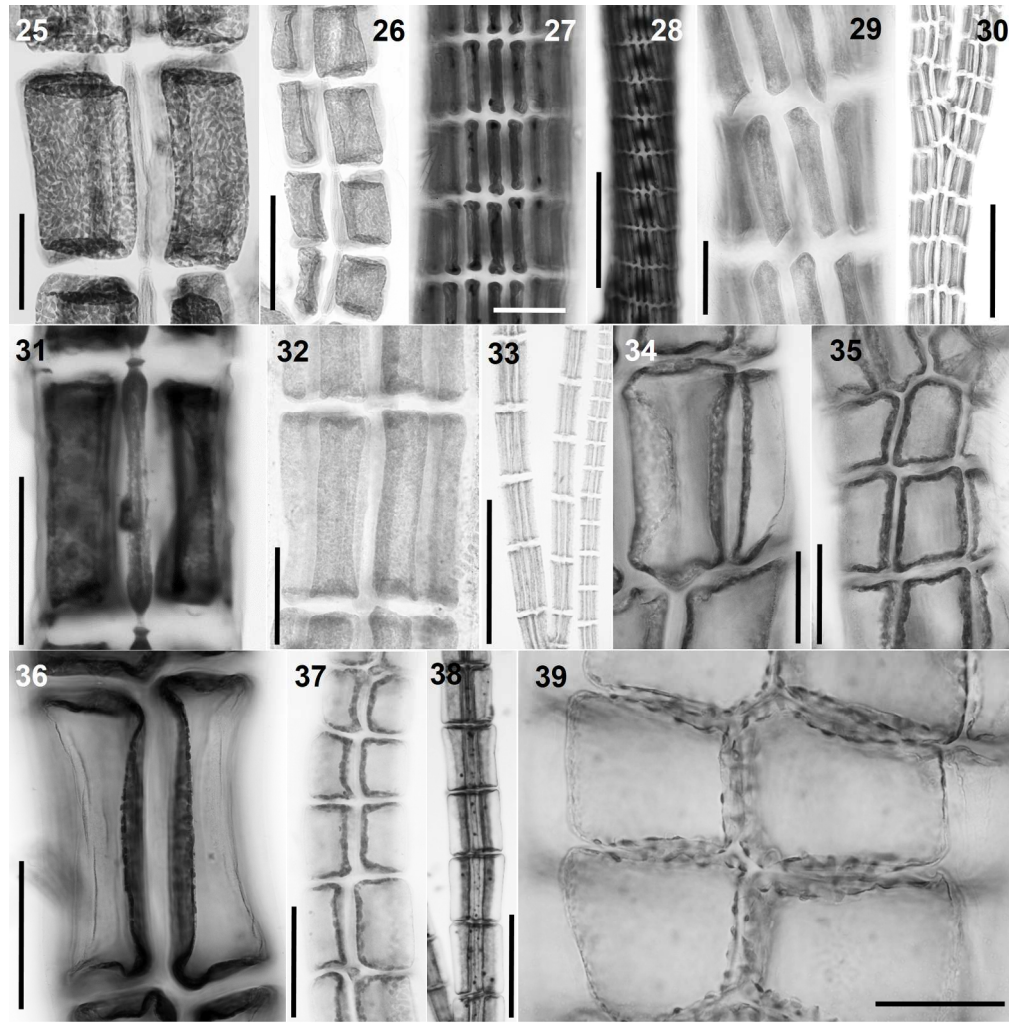


Figs 9-18. *Fernandosiphonia unilateralis* type material, the type species of *Fernandosiphonia*. Fig. 9. Herbarium specimen. Figs 10-11. Branches unilaterally arranged. Fig. 12. Axis with scar cells of trichoblasts (arrows). Figs 13-14. Surface view of pericentral cells with plastids lying only on the radial walls, so that the outer walls appear transparent (Fig. 13, arrows) and cells have a dark flank (Fig. 14). Fig. 15. Young spermatangial branch formed on the first dichotomy of a trichoblast, remaining the other vegetative branch (arrow). Fig. 16. Procarp (su = supporting cell; cp = carpogonium). Fig. 17. Cystocarp. Fig. 18. Tetrasporangia arranged in short spiral series. Scale bars: Fig. 9, 3 cm; Fig. 10, 2 mm; Fig. 11, 450  $\mu\text{m}$ ; Figs 12, 14, 17 and 18, 100  $\mu\text{m}$ ; Figs 13 and 15, 40  $\mu\text{m}$ ; Fig. 16, 20  $\mu\text{m}$ .

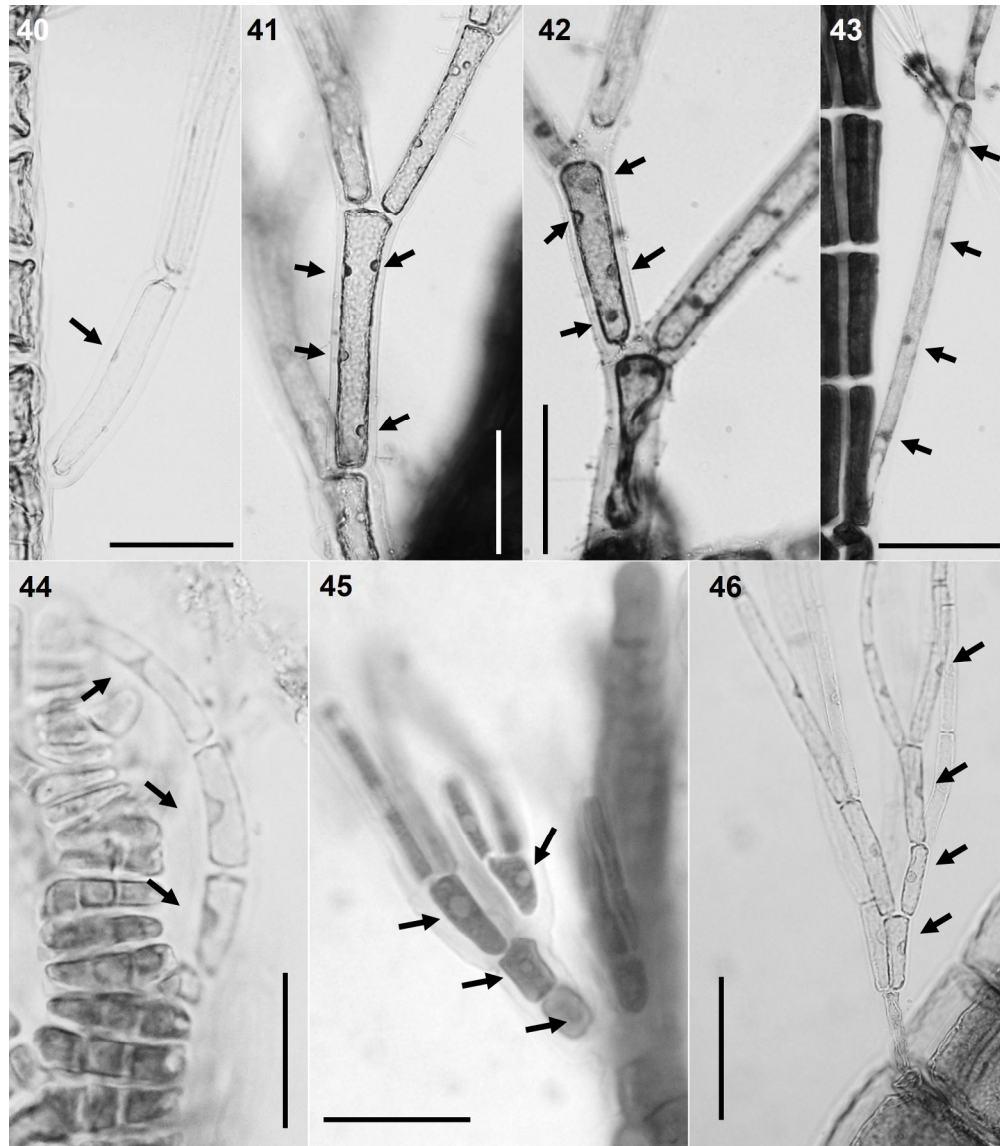


Figs 19-24. Rhizoid anatomy in the Polysiphoniaeae. In open connection with pericentral cells in *Polysiphonia stricta* (Fig. 19, *Polysiphonia sensu stricto* clade 1). Cut off from pericentral cells in *P. foetidissima* (Fig. 20, Vertebrata clade), *P. denudata* (Fig. 21, Carradoriella clade), *Polysiphonia* sp. (Fig. 22, Streblocladia clade), *P. schneideri* (Fig. 23, *P. schneideri* clade) and *P. incompta* (Fig. 24, Melanothamnus clade). Scale bars: Figs 19-23, 100  $\mu$ m; Fig. 24, 500  $\mu$ m.

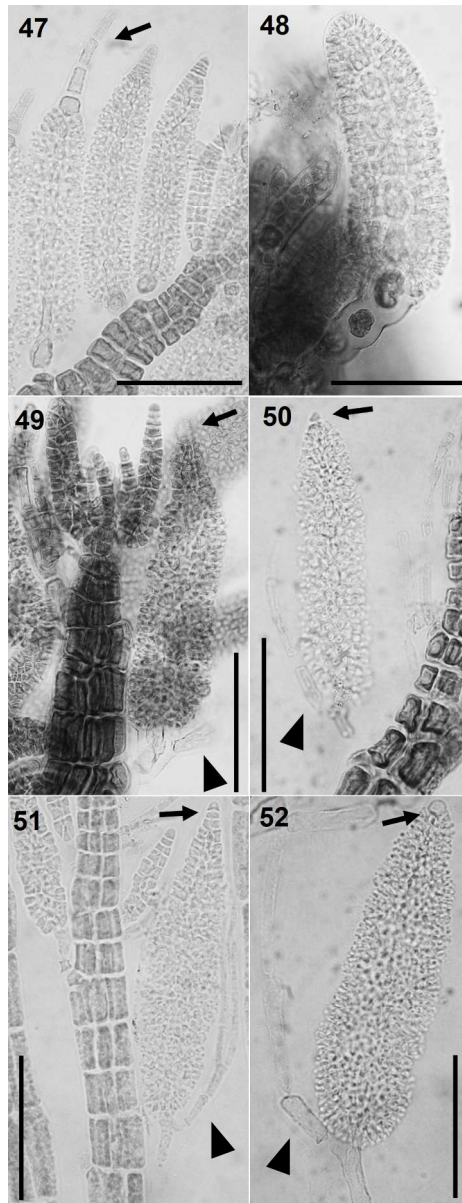




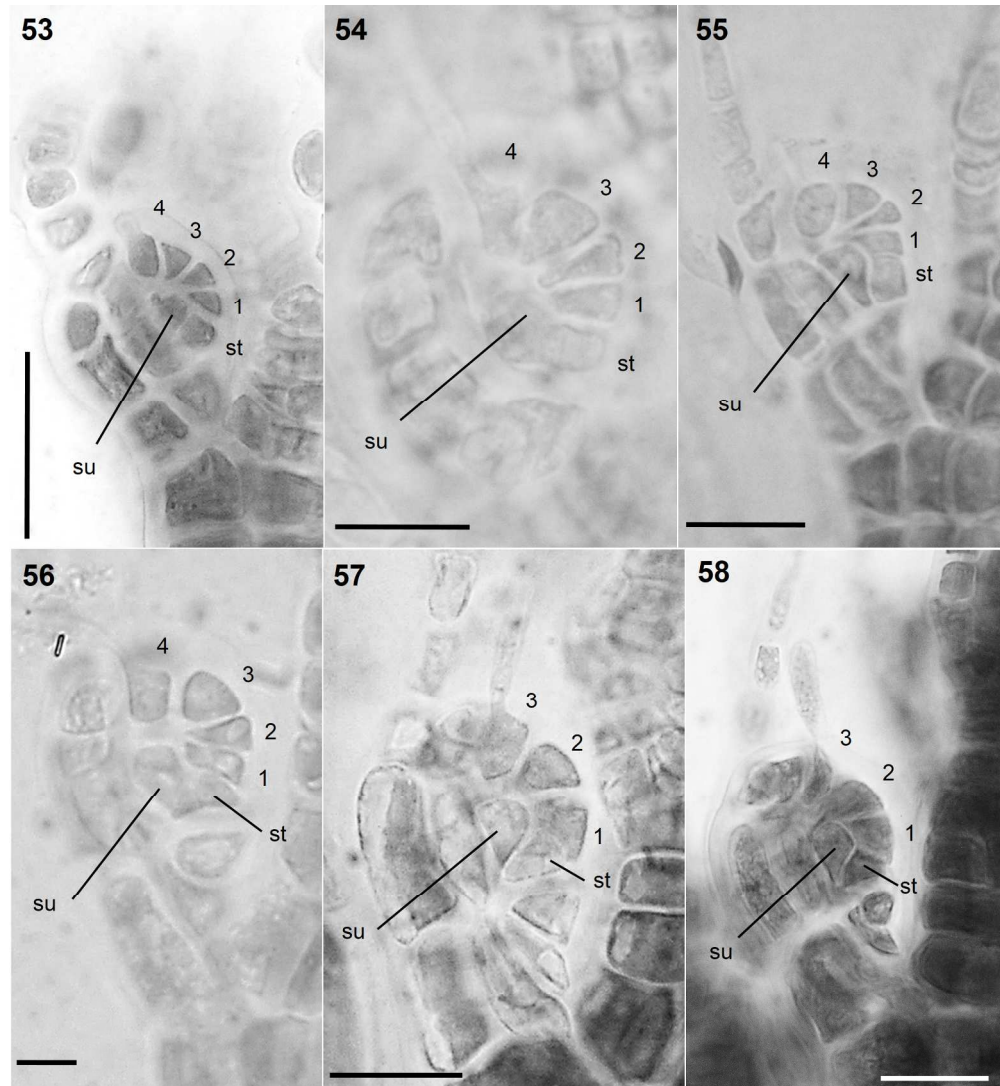
Figs 25-39. Plastid arrangement in the Polysiphoniaeae. Scattered against all cell walls of the pericentral cells in *Polysiphonia stricta* (Figs 25-26, *Polysiphonia sensu stricto* clade 1), *Vertebrata lanosa* (Figs 27-28, *Vertebrata* clade), *P. virgata* (Figs 29-30, *Carradoriella* clade), *Polysiphonia* sp. (Fig. 31, *Strebloladia* clade) and *P. schneideri* (Figs 32-33, *P. schneideri* clade). Lying exclusively on the radial walls of the pericentral cells in species of the *Melanothamnus* clade: *Neosiphonia collabens* (Figs 34-35), *N. harveyi* (Figs 36-38) and *P. forfex* (Fig. 39). Scale bars: Figs 25, 27, 29, 38 and 39, 500  $\mu\text{m}$ ; Figs 26, 28 and 30, 800  $\mu\text{m}$ ; Figs 31, 32, 34, 35 and 37, 100  $\mu\text{m}$ ; Fig. 33, 300  $\mu\text{m}$ ; Fig. 36, 50  $\mu\text{m}$ .



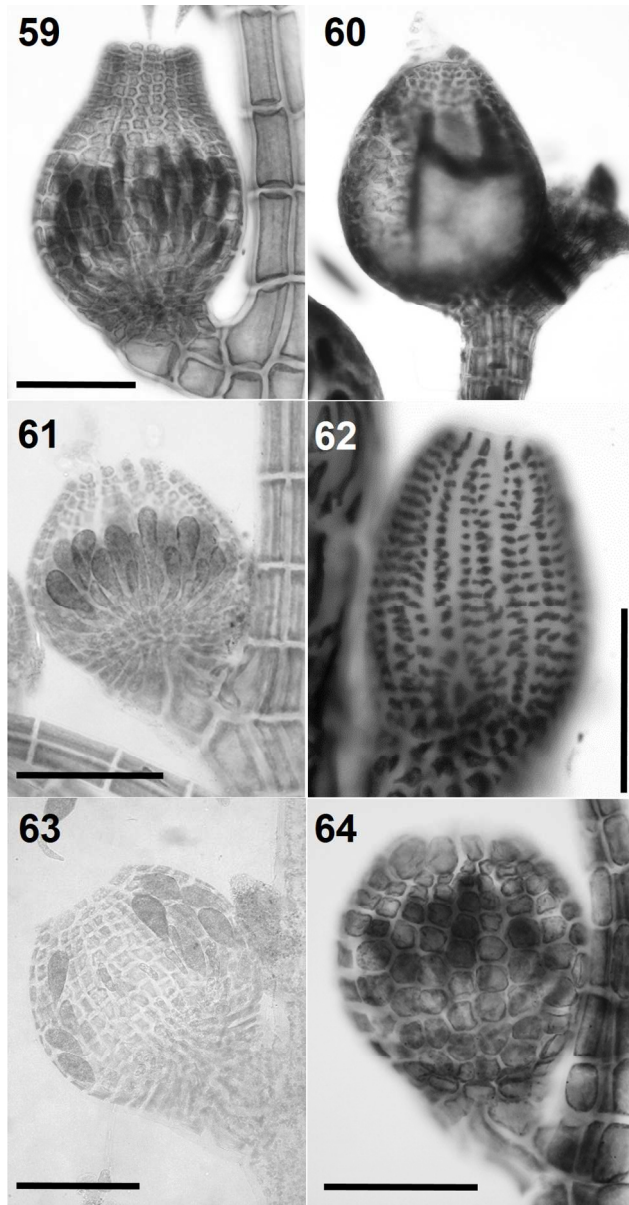
Figs 40-46. Trichoblast nuclei (arrows) in the Polysiphoniaeae. Uninucleate trichoblast cells in *Polysiphonia scopulorum* (Fig. 40, *Polysiphonia* sensu stricto clade 1), *P. denudata* (Fig. 44, *Carradoriella* clade), *P. schneideri* (Fig. 45, *P. schneideri* clade) and *P. blandii* (Fig. 46, *Melanothamnus* clade). Multinucleate trichoblast cells in species of the *Vertebrata* clade: *P. nigra* (Fig. 41), *Boergeseniella fruticulosa* (Fig. 42) and *P. foetidissima* (Fig. 43). Scale bars: Figs 40-43, 60  $\mu\text{m}$ , Fig. 44, 30  $\mu\text{m}$ ; Fig. 45, 20  $\mu\text{m}$ ; Fig. 46, 100  $\mu\text{m}$ .



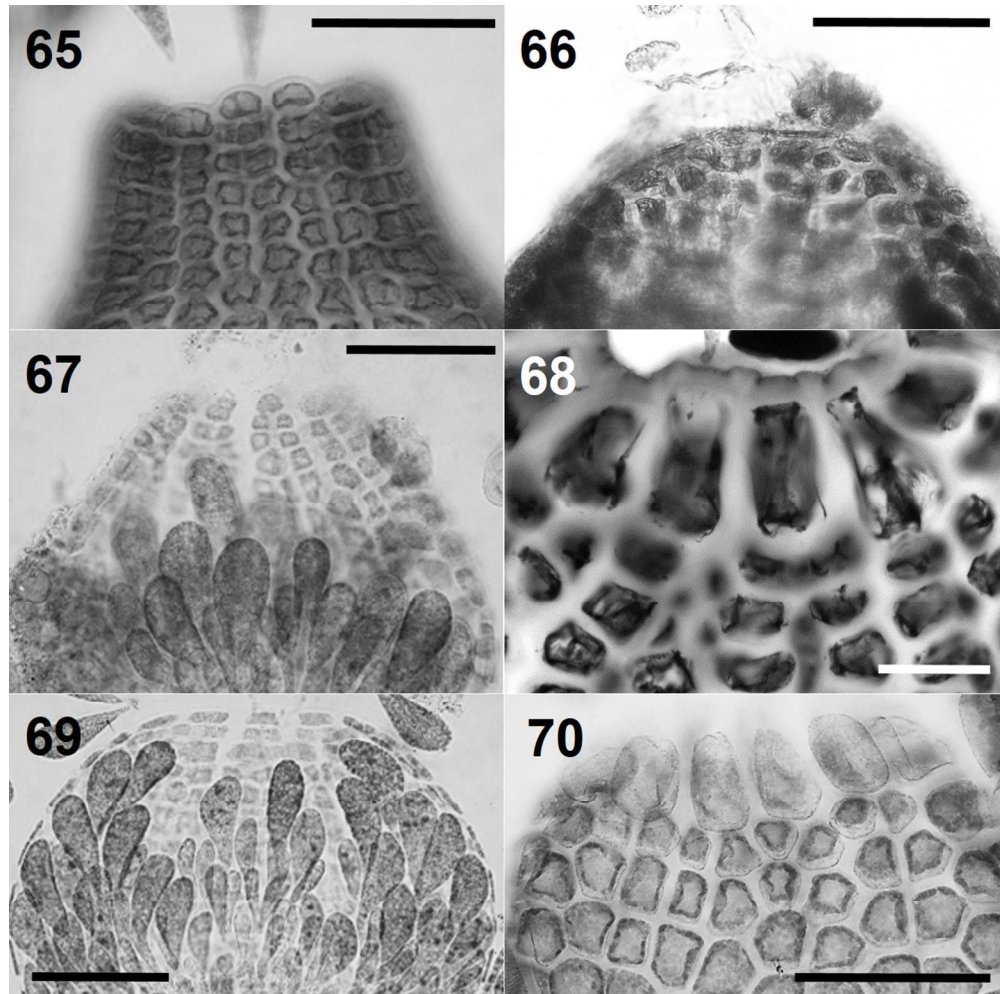
Figs 47-52. Spermatangial branches in the Polysiphonieae. Replacing trichoblasts and with sterile apical filaments in *Polysiphonia stricta* (Fig. 47, *Polysiphonia sensu stricto* clade 1). Replacing trichoblasts and lacking sterile apical cells in *Vertebrata lanosa* (Fig. 48, *Vertebrata* clade). On a branch of a trichoblast and with sterile apical cells in *P. fucoides* (Fig. 49, *Vertebrata* clade), *P. denudata* (Fig. 50, *Carradoriella* clade), *P. schneideri* (Fig. 51, *P. schneideri* clade) and *Neosiphonia harveyi* (Fig. 52, *Melanothamnus* clade). Scale bars: 100  $\mu\text{m}$ . Arrows show the apical sterile cells and arrowheads the sterile branch of fertile trichoblasts.



Figs 53-58. Carposiphonoid branches in the Polysiphoniaeae. Four-celled in *Polysiphonia stricta* (Fig. 53, *Polysiphonia sensu stricto* clade 1), *P. nigra* (Fig. 54, Vertebrata clade), *P. denudata* (Fig. 55, Carradoriella clade) and *P. schneideri* (Fig. 56, *P. schneideri* clade). Three-celled in species of the Melanothamnus clade: *Neosiphonia harveyi* (Fig. 57) and *P. blandii* (Fig. 58). Su = supporting cell; st = sterile basal cell; 1-4 cells of carposiphonoid branches. Scale bars: Fig. 53, 30  $\mu\text{m}$ ; Figs 54-58, 20  $\mu\text{m}$ .

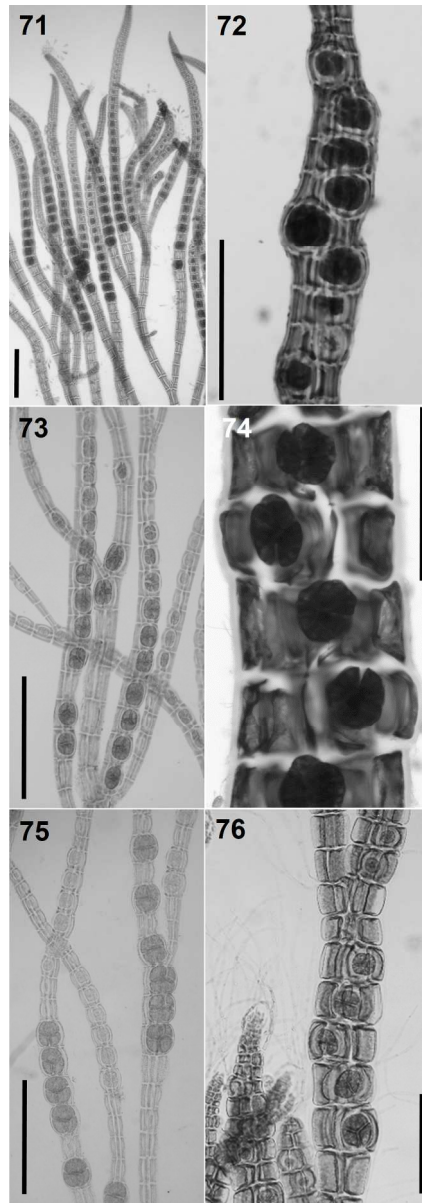


Figs 59-64. Cystocarps in the Polysiphonieae. Urceolate in *Polysiphonia stricta* (Fig. 59, *Polysiphonia sensu stricto* clade 1). Ovoid in *Vertebrata lanosa* (Fig. 60, *Vertebrata* clade), *P. denudata* (Fig. 61, *Carradoriella* clade), *Streblocladia glomerulata* (Fig. 62, *Streblocladia* clade). Globose in *Polysiphonia schneideri* (Fig. 63, *P. schneideri* clade) and *Neosiphonia collabens* (Fig. 64, *Melanothamnus* clade). Scale bars: Figs 59-62 and 64, 200  $\mu\text{m}$ ; Fig. 63, 100  $\mu\text{m}$ .



Figs 65-70. Cells surrounding the ostiole in the Polysiphoniaeae. Similar or slightly larger than the cells of the pericarp immediately below in *Polysiphonia stricta* (Fig. 65, *Polysiphonia sensu stricto* clade 1), *Vertebrata lanosa* (Fig. 66, *Vertebrata* clade), *P. denudata* (Fig. 67, *Carradoriella* clade), and *P. schneideri* (Fig. 69, *P. schneideri* clade). They are much larger in *Streblocladia glomerulata* (Fig. 68, *Streblocladia* clade) and *Neosiphonia collabens* (Fig. 70, *Melanothamnus* clade). Scale bars: Figs 65-68 and 70, 100  $\mu\text{m}$ ; Fig. 69, 60  $\mu\text{m}$ .





Figs 71-76. Tetrasporangia in the Polysiphoniaeae. Forming long straight series in *Polysiphonia stricta* (Fig. 71, *Polysiphonia sensu stricto* clade 1). Forming spiral series in *Vetebrata lanosa* (Fig. 72, *Vertebrata* clade), *Polysiphonia* sp. (Fig. 74, *Streblacladia* clade) and *Neosiphonia harveyi* (Fig. 76, *Melanothamnus* clade). Forming short straight series in *P. denudata* (Fig. 73, *Carradoriella* clade), and *P. schneideri* (Fig. 75, *P. schneideri* clade). Scale bars: Figs 71, 74 and 76, 200  $\mu\text{m}$ ; Figs 72, 73 and 75, 400  $\mu\text{m}$ .

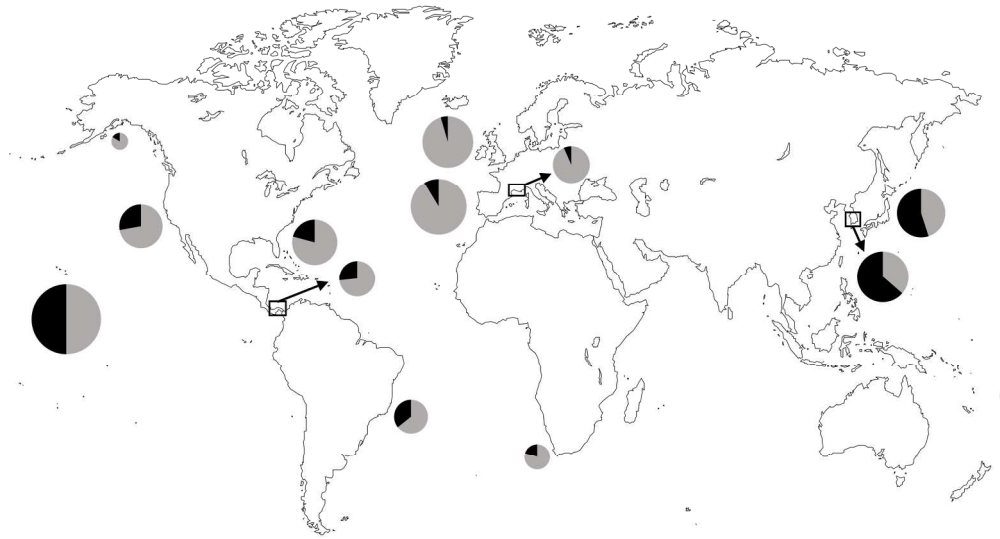


Fig. 77. World map representing the proportion of *Fernandosiphonia* (black) and other Polysiphoniae (grey) species in selected regions where the Polysiphoniae were studied in detail. Data were obtained from the following references after updating the species names: Alaska: Lindstrom (<http://www.seaweedsofalaska.com>); Brazil (Espírito Santo-São Paulo): Guimâraes et al. (2004); Hawaii: Abbott (1999); Japan: Yoshida (1998); Korea: Nam & Kang (2012); Panama: Mamoozadeh & Freshwater (2012); Spain (Galicia): Bárbara et al. (2005); British Isles: Maggs & Hommersand (1993).



Table S1. Sample information for the species included in the phylogenetic analysis.

Species (current name)	Publication or collection data and herbarium voucher for new sequences	GenBank accession number	
		<i>rbcL</i>	SSU
<i>Boergeseniella fruticulosa</i> (Wulfen) Kylin	Bárbara <i>et al.</i> (2013) / Choi <i>et al.</i> (2001)	JX828161	AF427526
<i>Boergeseniella thuyoides</i> (Harvey) Kylin	Bárbara <i>et al.</i> (2013)	JX828125	JX828165
<i>Brongniartella australis</i> (C.Agardh) F.Schmitz	Pope's Eye, Port Phillip Bay, Victoria Australia, 1.xii.2014, P. Díaz-Tapia & V. Marcelino; MEL	KX499546	KX499570
<i>Brongniartella byssoides</i> (Goodenough & Woodward) F.Schmitz	Yang <i>et al.</i> (2016) / Fanan Head, Donegal, Ireland, 15.vi.2015, P. Díaz-Tapia & C. Maggs; SANT 31111	DQ787584	KX499571
<i>Bryocladia cuspidata</i> (J.Agardh) De Toni	Lin <i>et al.</i> (2001)	AF259498	-

<i>Ctenosiphonia hypnoides</i> (Welwitsch ex J.Agardh) Falkenberg	Ensenada Cegoñas, Lugo, Spain, 15.vii.2010, P. Díaz-Tapia & I. Bárbara; SANT 24410	KX499547	-
<i>Enelittosiphonia stimpsonii</i> (Harvey) Kudo & Masuda	Bárbara <i>et al.</i> (2013) / Choi <i>et al.</i> (2001)	JX828126	AF427527
<i>Fernandosiphonia unilateralis</i> Levring	Juan Fernández, Chile, E. Macayo; SANT 31104-6	KX499549-52	KX499572-3
<i>Fernandosiphonia unilateralis</i> Levring	Type material, GB	KX499553	-
<i>Herposiphonia parca</i> Setchell	Bárbara <i>et al.</i> (2013)	-	JX828166
<i>Lampisiphonia iberica</i> Bárbara, Secilla, Díaz & H.-G. Choi	Bárbara <i>et al.</i> (2013)	JX828129	JX828168
<i>Leptosiphonia schousboei</i> (Thuret) Kylin	Bárbara <i>et al.</i> (2013)	JX828133	JX828170
<i>Lophosiphonia reptabunda</i> (Suhr) Kylin	Zumaia, Basque Country, Spain, 18.iii.2011, P. Díaz-Tapia & I. Bárbara;	KX499554	KX499574

	SANT 25139		
<i>Melanothamnus somalensis</i> Bornet & Falkenberg	Raaha Bay, Oman, 12.ix.2001, M. Wynne; MICH 662274	KX499555	-
<i>Melanothamnus afaqhusainii</i> Bornet & Falkenberg	Savoie & Saunders (2016, as <i>M. somalensis</i> )	KU564460	-
<i>N. teradomariensis</i> (M. Noda) M.S. Kim & I.K. Lee	Bárbara <i>et al.</i> (2013)	JX828136	JX828174
<i>Neosiphonia bajacali</i> (Hollenberg) N.R.Mamoozadeh & D.W.Freshwater	Mamoozadeh & Freshwater (2011)	HM573572	HM560659
<i>Neosiphonia baliana</i> D.E.Bustamante, B.Y.Won & T.O.Cho	Bustamante <i>et al.</i> (2013)	KF146879	-
<i>Neosiphonia collabens</i> (C. Agardh) Díaz-Tapia & Bárbara	Bárbara <i>et al.</i> (2013, as <i>Streblocladia collabens</i> )	JX828157	JX828188
<i>Neosiphonia echinata</i> (Harvey) N.Mamoozadeh & D.W.Freshwater	Mamoozadeh & Freshwater (2011)	HM573559	HM560658

1 2 3 4 5 6 7 8 9	<i>Neosiphonia ferulacea</i> (Suhr ex J.Agardh) S.M.Guimarães & M.T.Fujii	Mamoozadeh & Freshwater (2011)	HM573584	-
10 11 12	<i>Neosiphonia flavimarina</i> M.-S.Kim & I.K.Lee	Kim & Yang (2006)	DQ787481	-
13 14 15 16 17	<i>Neosiphonia harveyi</i> (J. Bailey) M.-S. Kim, H.-G. Choi, M.D. Guiry & G.W. Saunders	Bárbara <i>et al.</i> (2013)	JX828134	JX828172
18 19 20 21 22 23	<i>Neosiphonia peruviana</i> D.E.Bustamante, B.Y.Won, M.E.Ramirez & T.O.Cho	Bustamante <i>et al.</i> (2012b)	JN989969	-
24 25 26 27 28	<i>Neosiphonia cf. savatieri</i> (Hariot) M.S.Kim & I.K.Lee	Onno, Okinawa, Japan, 10.xi.2003, C. Trowbridge; BM	KX499558	
29 30 31	<i>Neosiphonia silvae</i> D.E.Bustamante, B.Y.Won & T.O.Cho	Bustamante <i>et al.</i> (2013)	KF146878	-
32 33 34	<i>Neosiphonia ramireziae</i> D.E.Bustamante, B.Y.Won & T.O.Cho	Bustamante <i>et al.</i> (2012a)	KC493352	-
35 36 37 38 39	<i>Neosiphonia</i> sp.	Mamoozadeh & Freshwater (2011)	HM573573	HM560649

<i>Neosiphonia sphaerocarpa</i> (Børgesen) M.-S.Kim & I.K.Lee	Mamoozadeh & Freshwater (2011)	HM573569	-
<i>Neosiphonia thailandica</i> N.Muangmai & C.Kaewsuralikhit	Muangmai <i>et al.</i> (2014)	KM502785	-
<i>Neosiphonia tongatensis</i> (Harvey ex Kützing) M.-S.Kim & I.K.Lee	Mamoozadeh & Freshwater (2011)	HM573570	HM560642
<i>Neosiphonia yendoii</i> (Segi) M.S. Kim & I.K. Lee	Bárbara <i>et al.</i> (2013)	JX828137	JX828175
<i>Polysiphonia amplacapilli</i> B.Kim & M.S.Kim	Kim & Kim (2014)	KF479253	-
<i>Polysiphonia anomala</i> Hollenberg	Mamoozadeh & Freshwater (2011)	HM573550	-
<i>Polysiphonia aterrима</i> J.D.Hooker & Harvey	Stuercke & Freshwater (2010) / Mamoozadeh & Freshwater (2011)	GU385831	HM560638
<i>Polysiphonia atlantica</i> Kapraun & J.N. Norris	Bárbara <i>et al.</i> (2013)	JX828141	JX828179
<i>Polysiphonia atlantica</i> Kapraun & J.N. Norris	Stuercke & Freshwater (2008) / Mamoozadeh & Freshwater (2011)	-	HM560631
<i>Polysiphonia binneyi</i> Harvey	Mamoozadeh & Freshwater (2011)	HM573555	HM560636

<i>Polysiphonia blandii</i> Harvey	Sandrigham, Port Phillip Bay, Victoria Australia, 8.i.2015, P. Díaz-Tapia & M.Brookes; SANT 31107	KX499556	-
<i>Polysiphonia brodiei</i> (Dillwyn) Sprengel	McIvor <i>et al.</i> (2001) / Bárbara <i>et al.</i> (2013)	AF342916	JX828192
<i>Polysiphonia ceramiiformis</i> P.Crouan & H.Crouan	Wembury Point, Exeter, England, UK, 23.iii.2016, P. Díaz-Tapia & C. Maggs; SANT 31108	KX499568	KX499575
<i>Polysiphonia constricta</i> Womersley	Stuercke & Freshwater (2010) / Mamoozadeh & Freshwater (2011)	GU385832	HM560639
<i>Polysiphonia denudata</i> (Dillwyn) Grevill ex Harvey	Bárbara <i>et al.</i> (2013)	JX828143	JX828182
<i>Polysiphonia elongata</i> (Hudson) Sprengel	Bárbara <i>et al.</i> (2013) / Choi <i>et al.</i> (2001)	JX828162	AF427529
<i>Polysiphonia elongella</i> Harvey	McIvor <i>et al.</i> (2001)	AF342913	-

<i>Polysiphonia fibrata</i> (Dillwyn) Harvey	McIvor <i>et al.</i> (2001) / Kimmeridge, Dorset, England, UK, 6.vi.2015, P. Díaz- Tapia & C. Maggs; SANT 31110	AF342915	KX499576
<i>Polysiphonia fibrillosa</i> (Dillwyn) Sprengel	McIvor <i>et al.</i> (2001) / Swangea, Dorset, England, UK, 7.vi.2015, P. Díaz-Tapia & C. Maggs; SANT 31110	AF342912	KX499577
<i>Polysiphonia foetidissima</i> Cocks <i>ex</i> Bornet	Díaz-Tapia <i>et al.</i> (2013)	JQ653284	-
<i>Polysiphonia forfex</i> Harvey	Rottneest Island, Western Australia, 15.iii.2015, P. Díaz-Tapia & J. Costa; MEL	KX499565	-
<i>Polysiphonia freshwateri</i> D.Bustamante, B.Y.Won & T.O.Cho	Bustamante <i>et al.</i> (2015)	KJ957812	-
<i>Polysiphonia fucooides</i> (Hudson) Sprengel	Bárbara <i>et al.</i> (2013) / Mamoozadeh & Freshwater (2011)	JX828163	HM560627

<i>Polysiphonia furcellata</i> (C.Agardh) Harvey	Pwllheli, Wales, UK, 20.viii.1998, C. Maggs; BM	KX499559	-
<i>Polysiphonia cf. hancockii</i> (Dawson) R.E.Norris	Makung, Taiwan, v.2002, M. Hommersand & S.-M. Lin; BM	KX499548	-
<i>Polysiphonia havanensis</i> Montagne	Mamoozadeh & Freshwater (2011)	HM573554	HM560641
<i>Polysiphonia homoia</i> Setchell & N.L.Gardner	Mamoozadeh & Freshwater (2011)	HM573553	HM560653
<i>Polysiphonia incompta</i> Harvey	Preekstoel, Western Cape, South Africa, 25.xi.2014, K. Dixon & J. Ferreira; MEL	KX499560	-
<i>Polysiphonia isogona</i> Harvey	Mamoozadeh & Freshwater (2011) / Frankston, Dave's Bay, Port Phillip Bay, Victoria, Australia, 19.xi.2014, H. Verbruggen, MEL	HM573578	KX499578
<i>Polysiphonia kapraunii</i> B.Stuercke & D.W.Freshwater	Stuercke & Freshwater (2008) /	EU492920	HM560630



	Mamoozadeh & Freshwater (2011)		
<i>Polysiphonia lobophoralis</i> N.R.Mamoozadeh & D.W.Freshwater	Mamoozadeh & Freshwater (2011)	HM573551	HM560657
<i>Polysiphonia macrocarpa</i> (C.Agardh) Sprengel	Mamoozadeh & Freshwater (2011)	-	HM560632
<i>Polysiphonia cf. minutissima</i> Hollenberg	Sunabe, Okinawa, Japan, 6.xi.2003, C. Towbridge; BM	KX499557	-
<i>Polysiphonia morroides</i> B.Kim & M.S.Kim	Kim & Kim (2014)	KF479257	-
<i>Polysiphonia morrowii</i> Harvey	D' Archino <i>et al.</i> (2013) / Choi <i>et al.</i> (2001)	KC152488	AF427532
<i>Polysiphonia muelleriana</i> J.Agardh	Fujii <i>et al.</i> (2006)	AY588412	-
<i>Polysiphonia nigra</i> (Hudson) Batters	Bárbara <i>et al.</i> (2013) / Choi <i>et al.</i> (2001)	JX828164	AF427534
<i>Polysiphonia nuda</i> N.R.Mamoozadeh & D.W.Freshwater	Mamoozadeh & Freshwater (2011)	HM573571	HM560648
<i>Polysiphonia pacifica</i> Hollenberg	Kim <i>et al.</i> (2004) / Choi <i>et al.</i> (2001)	AY958162	AF427533

<i>Polysiphonia paniculata</i> Montagne	Kim <i>et al.</i> (2004) from Chile	AY396040	-
<i>Polysiphonia paniculata</i> Montagne	Zuccarello <i>et al.</i> (2004) from California	-	AY617144
<i>Polysiphonia pentamera</i> Hollenberg	Mamoozadeh & Freshwater (2011)	HM573564	HM560643
<i>Polysiphonia pseudovillum</i> Hollenberg	Mamoozadeh & Freshwater (2011)	HM573568	HM560650
<i>Polysiphonia sabulosa</i> B.Kim & M.S.Kim	Kim & Kim (2014)	KF479250	-
<i>Polysiphonia schneideri</i> B.Stuercke & D.W.Freshwater	Stuercke & Freshwater (2010) / Mamoozadeh & Freshwater (2011)	GU385836	HM560629
<i>Polysiphonia scopulorum</i> Harvey	Bárbara <i>et al.</i> (2013)	JX828149	JX828184
<i>Polysiphonia scopulorum</i> var. <i>villum</i> (J.Agardh) Hollenberg	Mamoozadeh & Freshwater (2011)	-	HM560633
<i>Polysiphonia sertularioides</i> (Grateloup) J.Agardh FL1	Mamoozadeh & Freshwater (2011)	HM573548	HM560646
<i>Polysiphonia sertularioides</i> (Grateloup) J.Agardh FL2	Mamoozadeh & Freshwater (2011)	HM573547	HM560652
<i>Polysiphonia sertularioides</i> (Grateloup) J.Agardh FL3	Mamoozadeh & Freshwater (2011)	HM573546	HM560647

<i>Polysiphonia</i> sp.	Carlile (2009)	GQ252567	-
<i>Polysiphonia</i> sp.	Sunabe, Okinawa, Japan, 9.iii.2003, C. Trowbridge; BM	KX499561	-
<i>Polysiphonia</i> sp.	Sail Rock, Taiwan, v.2002, M.H. Hommersand; BM	KX499562	-
<i>Polysiphonia</i> sp. Womersley	Mamoozadeh & Freshwater (2011, as <i>P.</i> <i>pernacola</i> )	HM573576	HM560637
<i>Polysiphonia</i> sp.	New Zealand, W. Freshwater, WNC 34062	KX499569	-
<i>Polysiphonia stricta</i> (Dillwyn) Greville	Bárbara <i>et al.</i> (2013) / Choi <i>et al.</i> (2001)	JX828151	AF427535
<i>Polysiphonia strictissima</i> J.D.Hooker & Harvey	Stuercke & Freshwater (2010) / Mamoozadeh & Freshwater (2011)	GU385833	-
<i>Polysiphonia subtilissima</i> Montagne	Lam <i>et al.</i> (2013) / Mamoozadeh &	JX294918	HM560634

	Freshwater (2011)		
<i>Polysiphonia subulifera</i> (C.Agardh) Harvey	Kingstown Bay, Co. Galway, Ireland, 22.ix.1999, C. Maggs; BM	KX499564	-
<i>Polysiphonia tripinnata</i> J.Agardh	Peinzás, Lugo, Spain, 18.ix.2008, P. Díaz- Tapia & I. Bárbara; SANT 22246	KX499566	-
<i>Polysiphonia urbana</i> Harvey	Shelley Beach, Eastern Cape, South Africa, 8.xii.2014, K. Dixon & J. Ferreira; MEL	KX499567	-
<i>Polysiphonia virgata</i> (C. Agardh) Sprengel	Bárbara <i>et al.</i> (2013)	JX828152	JX828185
<i>Xiphosiphonia pennata</i> (C. Agardh) Savoie & Saunders	Bárbara <i>et al.</i> (2013)	-	JX828187
<i>Strebl cladia glomerulata</i> (Montagne) Papenfuss	New Zealand, W. Freshwater; WNC 34061	KX499569	KX499579

<i>Symphyocladia latiuscula</i> (Harvey) Yamada	Kim <i>et al.</i> (2010)	GQ867072	-
<i>Symphyocladia linearis</i> (Okamura) Falkenberg	Bárbara <i>et al.</i> (2013)	JX828158	JX828189
<i>Symphyocladia lithophila</i> M.-S.Kim	Kim <i>et al.</i> (2010)	GQ867078	-
<i>Vertebrata lanosa</i> (Linnaeus) T. Christensen	Stuercke & Freshwater (2008) / Phillips <i>et al.</i> (2000)	EU492914	AF203886

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Table S2. List of herbarium specimens examined for comparison with *Melanothamnus* species

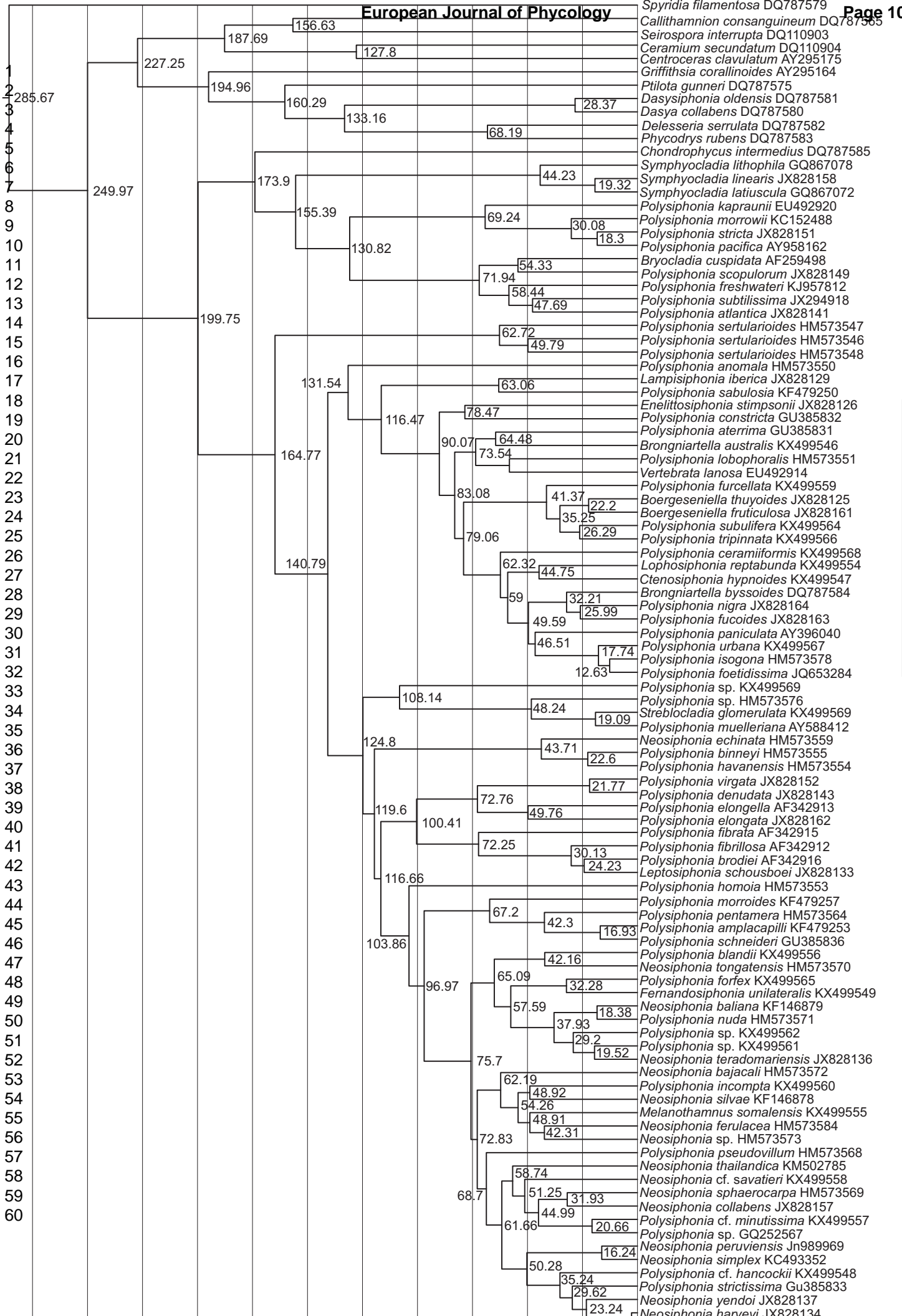
Species	Herbarium	Code
<i>Lophosiphonia mexicana</i> E.Y.Dawson	US	EYD430 (66781)
<i>Polysiphonia beaudettei</i> Hollenberg	US	EYD21379 (5219)
<i>Polysiphonia concinna</i> Hollenberg	US	GJH2015 (61210)
<i>Polysiphonia eastwoodae</i> Setchell & N.L.Gardner	US	55 (66788)
<i>Polysiphonia gorgoniae</i> Harvey	TCD	TCD0012804
<i>Polysiphonia harlandii</i> Harvey	TCD	TCD0011955
<i>Polysiphonia inconspicua</i> ( <i>P. confusa</i> Hollenberg)	US	GJH3285 (61222)
<i>Polysiphonia johnstonii</i> Setchell & N.L.Gardner	US	110 (66795)
<i>Polysiphonia poko</i> Hollenberg Hollenberg	US	GJH.65-82.6 (61243)
<i>Polysiphonia poko</i> var <i>longii</i>	US	2709.1 (61230)
<i>Polysiphonia profunda</i> Hollenberg	US	MSD19116AI1 (61231)
<i>Polysiphonia rubrorhiza</i> Hollenberg	US	18740D (48527)

Table S3. Percentage of bases that differ (down) and are identical (above) for the species sequences of the *Melanothamnus* clade included in our *rbcL* alignment.

	<i>Neosiphonia bajacali</i>	<i>Polysiphonia pseudovillum</i>	<i>Polysiphonia savatieri</i>	<i>Neosiphonia thailandica</i>	<i>Neosiphonia sp.</i>	<i>Neosiphonia silvae</i>	<i>Neosiphonia ferulacea</i>	<i>Polysiphonia sp.</i>	<i>Polysiphonia cf. minutissima</i>	<i>Polysiphonia blandii</i>	<i>Neosiphonia flavimarina</i>	<i>Neosiphonia harveyi</i>	<i>Neosiphonia tongatensis</i>	<i>Neosiphonia sphaerocarpa</i>	<i>Neosiphonia collabens</i>	<i>Neosiphonia peruviansis</i>	<i>Neosiphonia simplex (as ramirezii)</i>	<i>Neosiphonia simplex</i>	<i>Polysiphonia forfex</i>	<i>Fernandosiphonia unilateralis</i>	<i>Melanothamnus afaqhusainii</i>	<i>Melanothamnus somalensis</i>	<i>Fernandosiphonia cf. hancockii</i>	<i>Polysiphonia strictissima</i>	<i>Neosiphonia yendoii</i>	<i>Polysiphonia sp.</i>	<i>Neosiphonia baliانا</i>	<i>Polysiphonia sp.</i>	<i>Polysiphonia nuda</i>	<i>Polysiphonia incompta</i>	<i>Neosiphonia teradomariensis</i>					
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12	<i>Neosiphonia bajacali</i>	90.7	90.9	90.2	92.3	90.9	92.6	90.4	90.4	91.7	90.6	90.9	91.6	91.2	90.6	91.2	91.5	90.6	91	91.2	91.8	91.9	90.9	91.2	91.3	91.1	92	91.8	92.6	91.2	92.1					
13	<i>Polysiphonia pseudovillum</i>	9.3		91.9	92.8	92	92.4	92.8	92.4	92.1	93.1	92.2	92.4	92.2	92.4	93	93	91.7	92.8	92.4	93.1	93.3	92.1	93.2	92.3	91.4	92.3	92.6	92.8	91.8	92.8					
14	<i>Polysiphonia savatieri</i>	9.1	8.1		91.7	91.5	91.7	92.7	93.3	93.4	91.4	93	93.1	91.7	93.6	92.9	92.5	92	91.4	91.8	92.2	91.4	92.1	92.4	92.2	93.2	91.7	91.6	91.9	92.7	90.6	92.5				
15	<i>Neosiphonia thailandica</i>	9.8	7.2	8.3		92.4	92.6	92.5	93.1	92.5	93	92.4	92.9	91.7	92.7	93.3	93.2	92.7	90.5	92.3	92	92.1	92	91.8	92.8	93.5	91.7	91.8	92.9	92.9	91	93.1				
16	<i>Neosiphonia sp.</i>	7.7	8	8.5	7.6		92.8	93.6	91.8	91.3	92.6	92	92.2	92.7	92.5	92.6	92.4	92.2	91.4	92.2	91.4	93.3	93.5	92	92.5	92.3	91.5	91.4	92.8	92.9	92.4	92.9				
17	<i>Neosiphonia silvae</i>	9.1	7.6	8.3	7.4	7.2		92.8	92.7	92	92.8	91.9	92.2	92.4	92.1	91.8	93.1	92.9	92.2	91.8	91.2	93.6	93.7	91.4	91.9	92.4	90.7	91.7	91.7	91.9	92.5	92.1				
18	<i>Neosiphonia ferulacea</i>	7.4	7.2	7.3	7.5	6.4	7.2		92	91.8	93.8	92.9	92.9	93.3	92.6	92.3	93.3	93.2	90.9	93.2	93.1	94	94.1	92.6	92.8	93.1	92	92.6	93.3	93.5	93	93.7				
19	<i>Polysiphonia sp.</i>	9.6	7.6	6.7	6.9	8.2	7.3	8		96.5	92	92.7	93.5	92.2	94	94.3	94	93.5	91.5	92.6	92.3	91.6	92.5	92.7	92.6	93.3	92	93.1	92.9	92.5	91.8	93.8				
20	<i>Polysiphonia cf. minutissima</i>	9.6	7.9	6.6	7.5	8.7	8	8.2	3.5		91.7	91.9	92.3	92	93.5	93.2	92.7	91.9	91.4	91.5	91.8	91.4	91.7	91.9	91.3	92.6	91	91.1	91.4	92.2	90.2	92.1				
21	<i>Polysiphonia blandii</i>	8.3	6.9	8.6	7	7.4	7.2	6.2	8	8.3		91.8	92.3	95.8	92.1	91.9	93	92.6	90.9	94	92.1	92.8	92.6	92.2	92.8	93.3	92.3	91.7	93.4	93.3	93.3	93.4				
22	<i>Neosiphonia flavimarina</i>	9.4	7.8	7	7.6	8	8.1	7.1	7.3	8.1	8.2		99.6	93.7	92.8	93.4	93.7	93.7	92.5	92.9	93.4	92.4	92.9	95.7	96.1	95.8	91.6	92.4	92.7	93.2	91.6	93.7				
23	<i>Neosiphonia harveyi</i>	9.1	7.6	6.9	7.1	7.8	7.8	7.1	6.5	7.7	7.7	0.4		93.9	93	94.3	94.2	94	92.8	93.3	93.3	92.5	93.3	95.8	96.7	96.7	91.9	93.5	92.9	93.1	92	94.3				
24	<i>Neosiphonia tongatensis</i>	8.4	7.6	8.3	8.3	7.3	7.6	6.7	7.8	8	4.2	6.3	6.1		92.1	92.4	93.5	93.3	91.9	93	92.7	93.2	93.3	93.1	93.6	93.4	92.9	93.7	94.2	94.1	91.9	94.3				
25	<i>Neosiphonia sphaerocarpa</i>	8.8	7.8	6.4	7.3	7.5	7.9	7.4	6	6.5	7.9	7.2	7	7.9		95.5	93.7	93.6	92.7	93.2	92.5	92.3	93	93.4	93	93.7	92.6	91.8	93.2	93	91.8	93.6				
26	<i>Neosiphonia collabens</i>	9.4	7.6	7.1	6.7	7.4	8.2	7.7	5.7	6.8	8.1	6.6	5.7	7.6	4.5		94.1	93.5	92.5	93.1	91.8	92	92.5	93.4	93.4	94.5	92	92.5	93	92.7	92.3	94.1				
27	<i>Neosiphonia peruviansis</i>	8.8	7	7.5	6.8	7.6	6.9	6.7	6	7.3	7	6.3	5.8	6.5	6.3	5.9		97.8	96.6	93.5	93.1	92.7	93.4	94.3	95	94.2	91.9	93.3	93.7	93.4	92.2	94.5				
28	<i>Neosiphonia simplex (as ramirezii)</i>	8.5	7	8	7.3	7.8	7.1	6.8	6.5	8.1	7.4	6.3	6	6.7	6.4	6.5	2.2		99	93.5	93.7	92.7	93.4	93.8	95	93.5	91.4	93	93.6	92.7	92.4	93.7				
29	<i>Neosiphonia simplex</i>	9.4	8.3	8.6	9.5	8.6	7.8	8.1	8.5	8.6	9.1	7.5	7.2	8.1	7.3	7.5	3.4	1		92.2	92.7	91.7	92.5	92.2	93.7	92.1	89.9	91.1	91.8	91.7	92.1	91.7				
30	<i>Polysiphonia forfex</i>	9	7.2	8.2	7.7	7.8	8.2	6.8	7.4	8.5	6	7.1	6.7	7	6.8	6.9	6.5	6.5	7.8		95.3	92.6	93.1	92.8	93.4	93.8	92.3	93.5	94.2	93.3	91.8	94.8				
31	<i>Fernandosiphonia unilateralis</i>	8.8	7.6	7.8	8	8.6	8.8	6.9	7.7	8.2	7.9	6.6	6.7	7.3	7.5	8.2	6.9	6.3	7.3	4.7		91.3	91.9	92.8	93.2	93.4	91.4	93.5	93	92.9	91.2	93.4				
32	<i>Melanothamnus afaqhusainii</i>	8.2	6.9	8.6	7.9	6.7	6.4	6	8.4	8.6	7.2	7.6	7.5	6.8	7.7	8	7.3	7.3	8.3	7.4	8.7		98.6	91.9	92.7	92.4	91.6	92.9	93.7	93.2	93.1	93.3				
33	<i>Melanothamnus somalensis</i>	8.1	6.7	7.9	8	6.5	6.3	5.9	7.5	8.3	7.4	7.1	6.7	6.7	7	7.5	6.6	6.6	7.5	6.9	8.1	1.4		92.7	93.5	93	92	93.2	94.1	93.5	93.5	94.1				
34	<i>Fernandosiphonia cf. hancockii</i>	9.1	7.9	7.6	8.2	8	8.6	7.4	7.3	8.1	7.8	4.3	4.2	6.9	6.6	6.6	5.7	6.2	7.8	7.2	7.2	8.1	7.3		95.5	95.3	91.7	92.5	93	93	91.2	93.4				
35	<i>Polysiphonia strictissima</i>	8.8	6.8	7.8	7.2	7.5	8.1	7.2	7.4	8.7	7.2	3.9	3.3	6.4	7	6.6	5	5	6.3	6.6	6.8	7.3	6.5	4.5		96.1	91.3	93.8	93.3	93.2	92.2	93.9				
36	<i>Neosiphonia yendoii</i>	8.7	7.7	6.8	6.5	7.7	7.6	6.9	6.7	7.4	6.7	4.2	3.3	6.6	6.3	5.5	5.8	6.5	7.9	6.2	6.6	7.6	7	4.7	3.9		91.5	93.3	92.7	93.2	92.5	94.1				
37	<i>Polysiphonia sp.</i>	8.9	8.6	8.3	8.3	8.5	9.3	8	8	9	7.7	8.4	8.1	7.1	7.4	8	8.1	8.6	10.1	7.7	8.6	8.4	8	8.3	8.7	8.5		93.8	95.8	94.5	90.3	95.3				
38	<i>Neosiphonia baliانا</i>	8	7.7	8.4	8.2	8.6	8.3	7.4	6.9	8.9	8.3	7.6	6.5	6.3	8.2	7.5	6.7	7	8.9	6.5	6.5	7.1	6.8	7.5	6.2	6.7	6.2		95.6	97.4	91.4	96				
39	<i>Polysiphonia sp.</i>	8.2	7.4	8.1	7.1	7.2	8.3	6.7	7.1	8.6	6.6	7.3	7.1	5.8	6.8	7	6.3	6.4	8.2	5.8	7	6.3	5.9	7	6.7	7.3	4.2	4.4		96	92	97.9				
40	<i>Polysiphonia nuda</i>	7.4	7.2	7.3	7.1	7.1	8.1	6.5	7.5	7.8	6.7	6.8	6.9	5.9	7	7.3	6.6	7.3	8.3	6.7	7.1	6.8	6.5	7	6.8	6.8	5.5	2.6	4		92.4	96				
41	<i>Polysiphonia incompta</i>	8.8	8.2	9.4	9	7.6	7.5	7	8.2	9.8	6.7	8.4	8	8.1	8.2	7.7	7.8	7.6	7.9	8.2	8.8	6.9	6.5	8.8	7.8	7.5	9.7	8.6	8	7.6		92.5				
42	<i>Neosiphonia teradomariensis</i>	7.9	7.2	7.5	6.9	7.1	7.9	6.3	6.2	7.9	6.6	6.3	5.7	5.7	6.4	5.9	5.5	6.3	8.3	5.2	6.6	6.7	5.9	6.6	6.1	5.9	4.7	4	2.1	4	7.5					
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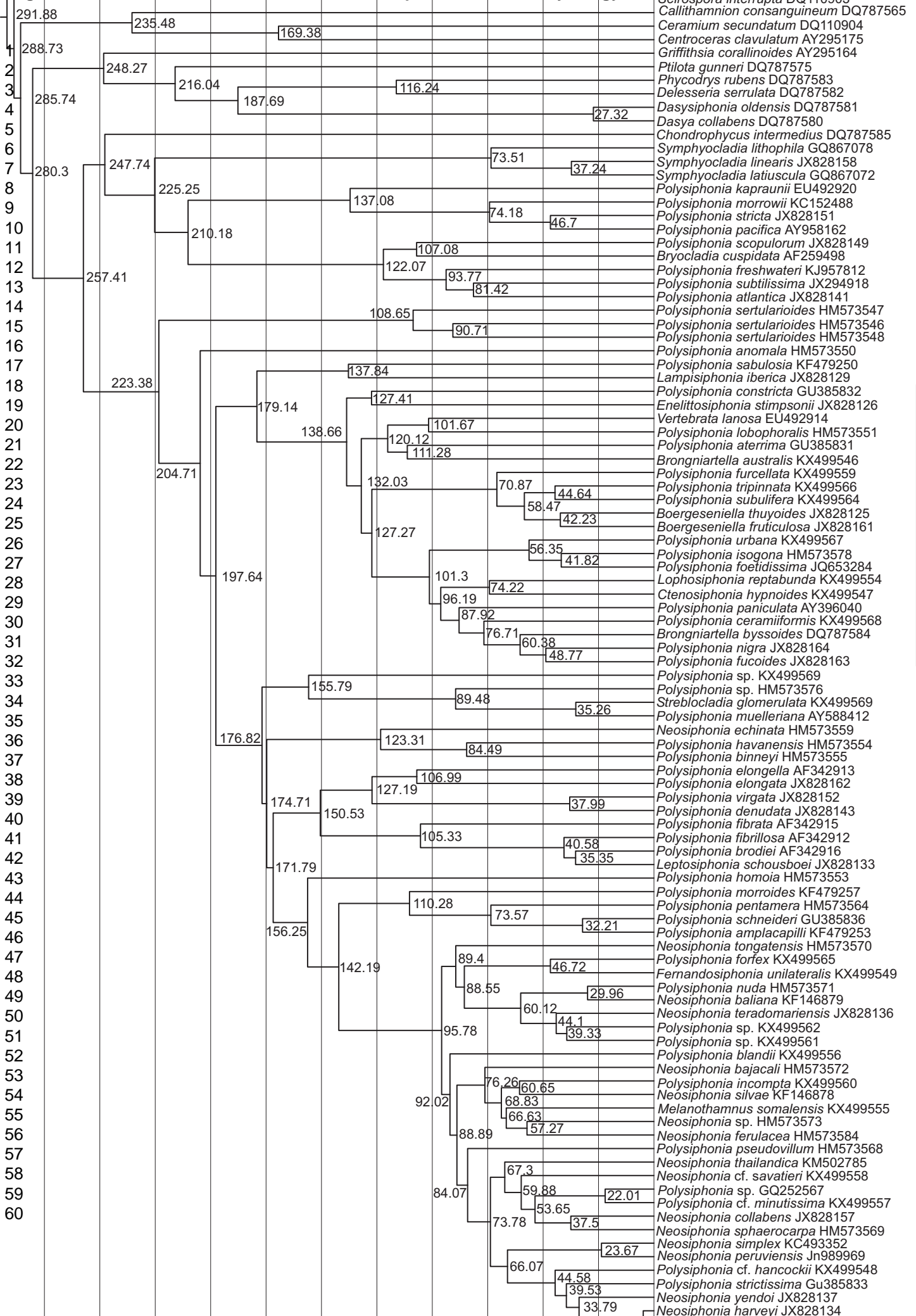
Table S4. Percentage of bases that differ (down) and are identical (above) for the species sequences of the *Vertebrata* clade included in our *rbcL* alignment.1  
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	<i>Vertebrata lanosa</i>	<i>Enelittosiphonia stimpsonii</i>	<i>Polysiphonia constricta</i>	<i>Polysiphonia aterrima</i>	<i>Polysiphonia lobophoralis</i>	<i>Boergeseniella fruticulosa</i>	<i>Boergeseniella thuyoides</i>	<i>Polysiphonia tripinnata</i>	<i>Polysiphonia furcellata</i>	<i>Polysiphonia subulifera</i>	<i>Brongniartella australis</i>	<i>Ctenosiphonia hypnoides</i>	<i>Lophosiphonia reptabunda</i>	<i>Polysiphonia simulans</i>	<i>Polysiphonia urbana</i>	<i>Polysiphonia foetidissima</i>	<i>Polysiphonia isogona</i>	<i>Polysiphonia paniculata</i>	<i>Polysiphonia fucooides</i>	<i>Brongniartella byssoides</i>	<i>Polysiphonia nigra</i>
<i>Vertebrata lanosa</i>		89.8	90.3	91.4	91.7	90.8	91.2	91.5	90.5	90	91.9	90.2	89.8	90.9	91.6	91.9	91.6	91.4	91	91.3	91.2
<i>Enelittosiphonia stimpsonii</i>	10.2		91.1	90.9	91.3	91.5	91.3	92.3	91.4	90.7	93.1	91.5	90.7	90.1	92.2	91.6	91.7	92.2	90.7	92.3	91.2
<i>Polysiphonia constricta</i>	9.7	8.9		91	91.2	91.6	91.8	91.7	91	90.7	92.2	91.1	90.4	91.3	92.7	92.5	92	91.5	91.1	91.6	91.4
<i>Polysiphonia aterrima</i>	8.6	9.1	9		92.4	91.6	92.2	91.7	92.2	91.4	93.2	90.9	90.8	91.6	92.6	92.2	92.8	92.1	91.7	91.7	91.6
<i>Polysiphonia lobophoralis</i>	8.3	8.7	8.8	7.6		91.7	92.7	90.5	90.9	90.8	93.4	90.5	91	91.6	91.7	91.5	91.3	90.7	90.3	91	91.1
<i>Boergeseniella fruticulosa</i>	9.2	8.5	8.4	8.4	8.3		97.4	96.6	95.3	95.4	93.6	91.9	91.4	92	92.9	92.4	92.1	92.2	92	92.8	92.5
<i>Boergeseniella thuyoides</i>	8.8	8.7	8.2	7.8	7.3	2.6		96.4	96.1	95.5	94.6	92.2	91.5	92.9	94	93.5	93	92.8	92.4	93.1	93.3
<i>Polysiphonia tripinnata</i>	8.5	7.7	8.3	8.3	9.5	3.4	3.6		95.7	96.3	93.8	92.3	90.5	93.6	94.5	94.1	94.5	93.3	93.8	94.1	94.1
<i>Polysiphonia furcellata</i>	9.5	8.6	9	7.8	9.1	4.7	3.9	4.3		94.7	93.4	91.7	90.5	92	93.5	92.9	92.4	92	91.5	92.4	92.2
<i>Polysiphonia subulifera</i>	10	9.3	9.3	8.6	9.2	4.6	4.5	3.7	5.3		92.9	91.6	90	91.4	92.8	91.9	91.5	90.9	91.2	91.7	91.6
<i>Brongniartella australis</i>	8.1	6.9	7.8	6.8	6.6	6.4	5.4	6.2	6.6	7.1		92.6	92.1	92.4	94.6	94	94	93.3	92.5	93.5	93.5
<i>Ctenosiphonia hypnoides</i>	9.8	8.5	8.9	9.1	9.5	8.1	7.8	7.7	8.3	8.4	7.4		92.3	92.4	93.4	93.1	92.8	92.5	92.2	92.8	92.5
<i>Lophosiphonia reptabunda</i>	10.2	9.3	9.6	9.2	9	8.6	8.5	9.5	9.5	10	7.9	7.7		92	92.8	92.2	92.4	92.2	91.4	92.1	92.3
<i>Polysiphonia simulans</i>	9.1	9.9	8.7	8.4	8.4	8	7.1	6.4	8	8.6	7.6	7.6	8		94.2	93.8	93.5	93.9	94.2	94.8	94.8
<i>Polysiphonia urbana</i>	8.4	7.8	7.3	7.4	8.3	7.1	6	5.5	6.5	7.2	5.4	6.6	7.2	5.8		97.9	97.4	94.7	94.5	95.3	95.2
<i>Polysiphonia foetidissima</i>	8.1	8.4	7.5	7.8	8.5	7.6	6.5	5.9	7.1	8.1	6	6.9	7.8	6.2	2.1		98.1	94.9	94.3	95.2	95.4
<i>Polysiphonia isogona</i>	8.4	8.3	8	7.2	8.7	7.9	7	5.5	7.6	8.5	6	7.2	7.6	6.5	2.6	1.9		95.1	94.2	94.8	95.2
<i>Polysiphonia paniculata</i>	8.6	7.8	8.5	7.9	9.3	7.8	7.2	6.7	8	9.1	6.7	7.5	7.8	6.1	5.3	5.1	4.9		94.3	95	95.5
<i>Polysiphonia fucooides</i>	9	9.3	8.9	8.3	9.7	8	7.6	6.2	8.5	8.8	7.5	7.8	8.6	5.8	5.5	5.7	5.8	5.7		95.7	96.4
<i>Brongniartella byssoides</i>	8.7	7.7	8.4	8.3	9	7.2	6.9	5.9	7.6	8.3	6.5	7.2	7.9	5.2	4.7	4.8	5.2	5	4.3		96.5
<i>Polysiphonia nigra</i>	8.8	8.8	8.6	8.4	8.9	7.5	6.7	5.9	7.8	8.4	6.5	7.5	7.7	5.2	4.8	4.6	4.8	4.5	3.6	3.5	



Vertebrata

Melanothamnus



Vertebrata

Melanothamnus

