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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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Running title: The genera *Melanothamnus* and *Vertebrata* (Rhodophyta)

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27 ABSTRACT

28

29 *Polysiphonia* is the largest genus of red algae, and several schemes subdividing it into smaller taxa
30 have been proposed since its original description. Most of these proposals were not generally
31 accepted, and currently the tribe Polysiphonieae consists of the large genus *Polysiphonia* (190
32 species), the segregate genus *Neosiphonia* (43 species), and 13 smaller genera (< 10 species each).
33 In this paper, phylogenetic relationships of the tribe Polysiphonieae are analysed, with particular
34 emphasis on the genera *Carradoriella*, *Fernandosiphonia*, *Melanothamnus*, *Neosiphonia*,
35 *Polysiphonia sensu stricto*, *Streblocladia* and *Vertebrata*. We evaluated the consistency of 14
36 selected morphological characters in the identified clades. Based on molecular phylogenetic (*rbcL*
37 and 18S genes) and morphological evidence, two speciose genera are recognized: *Vertebrata*
38 (including the type species of the genera *Ctenosiphonia*, *Enelittosiphonia*, *Boergeseniella* and
39 *Brongniartella*) and *Melanothamnus* (including the type species of the genera *Fernandosiphonia*
40 and *Neosiphonia*). Both genera are distinguished from other members of the Polysiphonieae by
41 synapomorphic characters, the emergence of which could have provided evolutionarily selective
42 advantages for these two lineages. In *Vertebrata* trichoblast cells are multinucleate, possibly
43 associated with the development of extraordinarily long photoprotective trichoblasts.
44 *Melanothamnus* has 3-celled carpogonial branches and plastids lying exclusively on radial walls of
45 the pericentral cells, which similarly may improve resistance to damage caused by excessive light.
46 Other relevant characters that are constant in each genus are also shared with other clades. The
47 evolutionary origin of the genera *Melanothamnus* and *Vertebrata* is estimated as 75.7-95.78 and
48 90.7-138.66 Ma, respectively. Despite arising in the Cretaceous, before the closure of the Tethys
49 Seaway, *Melanothamnus* is a predominantly Indo-Pacific genus and its near-absence from the
50 northeastern Atlantic is enigmatic. The nomenclatural implications of this work are that 46 species
51 are here transferred to *Melanothamnus*, six species are transferred to *Vertebrata*, and 13 names are
52 resurrected for *Vertebrata*.

53

54

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

56 *Polysiphonia*, red algae, time calibration

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61 INTRODUCTION

62 The Rhodomelaceae Areschoug is the largest family of red algae, currently including more than
 63 1,000 species (Guiry & Guiry, 2016). It consists of the tribes Amansieae Schmitz (1889),
 64 Bostrychieae Falkenberg (1901), Chondrieae Schmitz & Falkenberg (1897), Herposiphonieae
 65 Schmitz & Falkenberg (1897), Heterocladieae Falkenberg (1901), Laurencieae Schmitz (1889),
 66 Lophothalieae Schmitz & Falkenberg (1897), Neotenophyceae Kraft & I.A. Abbott (2002),
 67 Pleurostichidieae (Hommersand, 1963), Polysiphonieae Schmitz (1889), Polyzonieae Schmitz &
 68 Falkenberg (1897), Pterosiphonieae Falkenberg (1901), Rhodomeleae Schmitz & Falkenberg
 69 (1897), Sonderelleae L.E. Phillips (2001) and Streblocladieae nom. nud. (Hommersand, 1963;
 70 Kraft & Abbott, 2002; Womersley, 2003), of which the most speciose is the Polysiphonieae with
 71 over 300 species in 15 currently recognized genera (Guiry & Guiry, 2016).

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

85 The segregate genus *Neosiphonia* M.-S. Kim & I.K. Lee (Kim & Lee, 1999) has been widely
 86 accepted and is now the second largest in the Polysiphonieae (Guiry & Guiry, 2016). *Neosiphonia*

(type species: *N. flavimarina* 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 spiral arrangement (Kim & Lee, 1999). These features contrast markedly with the key characters of *Polysiphonia sensu stricto*, exemplified by the type species *P. stricta*: 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* 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* and *Polysiphonia virgata*, 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 *Neosiphonia* species and *Melanothamnus*

somalensis, the type species of the genus *Melanothamnus* Bornet & Falkenberg, which was regarded as *incertae sedis* (Falkenberg, 1901).

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

MATERIALS AND METHODS

Field collections, morphological studies and literature review

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

Type material of *Fernandosiphonia unilateralis* was obtained from the Herbarium, Botanical Museum, Göteborg, Sweden (GB) by correspondence with the curator. It consisted of four permanent slides, a herbarium sheet and liquid-preserved material. Furthermore, we studied recent collections from Juan Fernández Islands, the type locality. We also studied the type material in US and TCD of several species currently assigned to *Neosiphonia* (Table S2; herbarium

abbreviations as in Thiers, 2016) for which the key morphological characteristics (Table 1) could not be clearly ascertained from published literature, in order to determine their correct generic assignment. For this purpose, we exclusively considered the descriptions provided for material from type localities or near them. To ensure the accuracy of our interpretation of the genera, our concept of them is based on material of their type species obtained from their type localities. For *Streblocladia*, we used material of, and sequences from, the type species *S. glomerulata* from New Zealand. *Carradoriella* (i.e. *Polysiphonia virgata*) was obtained from the type locality in South Africa, and the type species of *Vertebrata* and *Melanothamnus* came from Ireland and Oman respectively.

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

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

Nomenclatural authorities for the species mentioned in the manuscript are provided in Tables 2-5 and S1-S2.

DNA extraction, PCR amplification and sequencing

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

At Queen's University Belfast, DNA was extracted from fresh, silica gel-dried or ethanol-preserved material using the Qiagen DNeasy Plant Mini Kit (Qiagen GmbH, Hilden, Germany), according to the manufacturer's instructions, or by a CTAB method, modified after Doyle & Doyle (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 μ M each of dATP, dCTP, dGTP and dTTP, 0.3 μ M of each primer, 2.5 mM MgCl₂, and 1.6 units of BiotaqTM DNA 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 and 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* 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 μ l, consisting of 5 μ l 5 $\times$ MyTaqTM reaction buffer, 0.7 μ l 10 μ M of forward and reverse primers, 0.125 μ l 1U μ l⁻¹ My TaqTM DNA Polymerase (Bioline), 17.475 μ l MilliQ® water and 1 μ l

template DNA. The PCR profile consisted of initial denaturation (93°C for 3 min); 35 cycles of denaturation (94°C for 30 s), primer annealing (45°C for 30 s), and extension (74°C for 90 s); and final extension (74°C for 5 min). The PCR products were purified and sequenced commercially by Macrogen.

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

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

Sequence alignment and phylogenetic analysis

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

Sequences were aligned using Muscle in Geneious 6.1.8 (Kearse *et al.*, 2012). Identical sequences and those that diverged by less than 1.1% were removed from the *rbcL* analysis, except for *Neosiphonia flavimarina* and *N. harveyi* (0.4% divergence), the two selected representatives of the “*N. japonica* complex” (Kim & Lee, 1999), which also includes *N. decumbens*, *N. harlandii* and *P. akkeshiensis* Segi (McIvor *et al.*, 2001; Kim & Yang, 2006; Savoie & Saunders, 2015; Bárbara *et al.*, 2013). Identical sequences were also removed from the 18S analysis. The sequences included in the final alignment were selected after considering their quality in terms of both length and the presence of ambiguous bases. Phylogenetic trees for *rbcL* and 18S were estimated with Maximum Likelihood (ML) using RAxML 8.1.6 (Stamatakis, 2014). GTR-Gamma was selected as the best nucleotide model; branch support was estimated with 100 bootstrap replicates. Three

species of *Symphyocladia* Falkenberg (in Schmitz & Falkenberg, 1897) were selected as the outgroup in the *rbcL* phylogeny and one species each of *Symphyocladia*, *Xiphosiphonia* Savoie & Saunders (2016) and *Herposiphonia* Nägeli (1846) were selected as outgroups for the 18S analysis. This outgroup selection was based on our phylogenomic analyses of the major lineages of the Rhodomelaceae which resolve a clade formed by the Herposiphonieae and Pterosiphonieae as sister to the Polysiphonieae (Díaz-Tapia *et al.*, 2015).

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

Trees were calibrated in geological time using relaxed molecular clock analyses. The calibration was derived from node ages inferred by Yang *et al.* (2016), which estimated the earliest split in Ceramiales (between *Spyridia* Harvey (1833) and the remaining Ceramiales) to be 292 Ma old (stdev $\approx$ 24.6 Ma). After adding the *rbcL* sequences of Ceramiales from the Yang *et al.* (2016) study to our alignment and setting *Spyridia* as the outgroup, node ages were inferred with two Bayesian methods. The first analysis used an autocorrelated model of molecular evolutionary rate change (Thorne & Kishino, 2002) as implemented in PhyloBayes v.3.3f (Lartillot *et al.*, 2009). The MCMC chain was run for 50k cycles, stationarity was assessed with Tracer, and the node ages 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 million generations, used a Yule tree prior, and an unpartitioned GTR+ Γ +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 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/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*: 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 *Streblacladia* 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 other taxa. *Polysiphonia sensu stricto* clades 1 and 2 are placed robustly together (99/1.00). Within the third clade, the *Vertebrata* clade receives full support, while support is lower for *Melanothamnus* (82/1.00). The sister relationship between the *Melanothamnus* and “*P.*”

293 *schneideri* clades is strongly supported in the 18S phylogeny. In addition, the *Carradoriella* and
 294 *Streblocladia* clades are highly supported.

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

299

300 Morphological observations

301

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

304

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

313

314 *Rhizoids*: The connection between the rhizoids and the pericentral cells from which they originate
 315 is a uniform character within each clade, so far as it can be observed (Table 1). Rhizoids are in
 316 open connection with pericentral cells in *Polysiphonia sensu stricto* (Fig. 19), while they are cut
 317 off from pericentral cells in the other clades (Figs 20-24). Observations on rhizoids cannot be
 318 made in mature specimens of some species, such as *Vertebrata lanosa* which is an obligate hemi-

parasite that lacks rhizoids, and *Fernandosiphonia unilateralis*, *Streblacladia 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. beaudettei*, *P. confusa*, *P. poko*, *P. profunda* and *P. rubrorhiza* have the plastids scattered within the cells, including against the outer wall cells.

344 *Branch/trichoblast arrangement*: Whether trichoblasts and/or branches are formed on every
 345 segment or are separated by naked segments is variable in three clades, *Melanothamnus*,
 346 *Carradoriella* and *Vertebrata*. Most species of the *Melanothamnus* clade have branches or
 347 trichoblasts on every segment, which is a key feature of *Neosiphonia*. However, there are
 348 exceptions in this clade such as *Neosiphonia collabens*, *Polysiphonia nuda* and *P. pseudovillum*
 349 from Panama, in which there are interspersed naked segments. Conversely, the formation of
 350 trichoblasts/branches with naked segments between them is a uniform character in the
 351 *Streblocladia*, “*Polysiphonia*” *schneideri* and *Polysiphonia sensu stricto* clades (Table 1). Within
 352 all clades except *Melanothamnus*, branches may form in a position axillary to trichoblasts, but
 353 although constant at the species level, this character is variable within clades. In the
 354 *Melanothamnus* clade this character is absent, and branches are never axillary.
 355
 356 *Trichoblast nuclei*: The proximal cells of trichoblasts are multinucleate in the *Vertebrata* clade
 357 (Table 1, Figs 41-43), with up to 8 or more nuclei in the basal cell and decreasing in number
 358 towards the apices, which can be uninucleate. The nuclei are uniformly distributed inside the cells,
 359 each appearing to have a domain within the cell. Conversely, all the cells of trichoblasts are
 360 uninucleate in other clades of the Polysiphonieae (Figs 40, 44-46). The only known exception is
 361 *Leptosiphonia schousboei*, which sometimes has two nuclei in the trichoblast cells.
 362
 363 *Branching pattern*: Despite the great significance previously placed on dorsiventral vs. radial
 364 branching in the Rhodomelaceae, this character varies within all our clades. A primary dorsiventral
 365 branching pattern characterizes some species of the clades *Melanothamnus* (*F. unilateralis* and *N.*
 366 *collabens*; Figs 10, 11), *Streblocladia* (*S. glomerulata*) and *Vertebrata* (*Ctenosiphonia hypnoides*)
 367 (Table 1). However, this characteristic is not significant in delineating these three genera, as our
 368 phylogenetic tree reveals that each of these four species is closely related to others that have
 369 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.

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 be observed only 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 *Melanothamnus* clade (Fig 70). However, *Neosiphonia harveyi* is an exception, and the cells of the ostiole in this species are only slightly larger than the other cells of the pericarp. This character

is also seen in *Streblocladia glomerulata* (Fig. 68). Conversely, the cells of the ostiole in the other four clades are uniformly similar to the cells below (Figs 65-67, 69).

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

DISCUSSION

Phylogenetic analysis

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

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 (1897), 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.

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

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

Taxonomic position of *Neosiphonia*, *Fernandosiphonia* and *Melanothamnus*

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

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

(2014), further studies are needed to clarify the generic placement of this unusual species, and meanwhile we propose to leave it in *Lophosiphonia* until more information is available.

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

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

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

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

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 (MAAs) 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

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. 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.*, 2013a). 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.*” *schneideri* clade 140 or 95 Ma (Figs S1, S2). The distribution resembles a Tethyan one that originated during the Cretaceous 125-75 Ma (Lüning, 1990; Hommersand, 2007) when the Tethys

Ocean formed a tropical girdle around the earth. Unlike typical Tethyan distributions, in addition to its wide occurrence throughout the tropics, *Melanothamnus* occupies more temperate regions in the North Pacific (e.g. Japan, Korea) and the South Pacific/Oceania (e.g. South Australia, New Zealand). The question of whether *Melanothamnus* failed to colonize the northeastern Atlantic as it opened up during the Cretaceous, or whether northeastern Atlantic lineages evolved but became extinct, perhaps during Pleistocene glaciations, cannot be answered at present.

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

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

Table 2. Genus *Vertebrata* with new combinations resulting from the present study printed in bold, followed by basionyms and taxonomic synonyms.

Binomial in <i>Vertebrata</i>	Type material
Basionym	Type locality
Synonyms	
<i>Vertebrata constricta</i> (Womersley) Díaz-Tapia & Maggs, comb. nov.	Holotype: AD A32927
<i>Polysiphonia constricta</i> Womersley (1979, 497-498; Southern Australian species of <i>Polysiphonia</i> Greville (Rhodophyta). <i>Australian Journal of Botany</i> , 27 : 459-528)	Kangaroo I., South Australia; 21.xi.1968
<i>Vertebrata foetidissima</i> (Cocks ex Bornet) Díaz-Tapia & Maggs, comb. nov.	Lectotype (Maggs & Hommersand,
<i>Polysiphonia foetidissima</i> Cocks ex Bornet (1892, pp. 314-315; Les algues de P. K. A. Schousboe.....	1993): PC 0146017
<i>Mémoires de la Société Nationale des Sciences naturelles et Mathématiques de Cherbourg</i> , 28 : 165-376)	Plymouth, England; undated
<i>Vertebrata isogona</i> (Harvey) Díaz-Tapia & Maggs, comb. nov.	Lectotype (Womersley, 1979): BM
<i>Polysiphonia isogona</i> Harvey (in Hooker 1855, p. 231; <i>The botany of the Antarctic voyage</i> Reeve,	1082304
London)	Blind Bay, Cook's Straits, New Zealand; viii.1849
<i>Vertebrata lobophoralis</i> (N.R.Mamoozadeh & D.W.Freshwater) D.W.Freshwater, comb. nov.	Holotype: US 217938
<i>Polysiphonia lobophoralis</i> N.R.Mamoozadeh & D.W.Freshwater (2012, pp. 331-333; <i>Polysiphonia sensu</i>	Bocas del Toro, Panama;

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

Table 3. Genus *Vertebrata* with resurrected names resulting from the present study printed in bold, followed by basionyms and taxonomic synonyms.

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

<i>Fucus fruticulosus</i> Wulfen	1993): Wulfen (1789), pl. 16, fig. 1
<i>Boergeseniella fruticulosa</i> (Wulfen) Kylin	Trieste [Tergestum], Adriatic
<i>Vertebrata fucoides</i> (Hudson) Kuntze	Neotype (Maggs & Hommersand,
<i>Conferva fucoides</i> Hudson	1993): BM 807101
<i>Polysiphonia fucoides</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	no. 39346
<i>Ctenosiphonia hypnoides</i> (Welwitsch) 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

***Vertebrata stimpsonii* (Harvey) Kuntze**

Holotype: TCD 11956

Polysiphonia stimpsonii Harvey

Hakodate Bay, Japan

Enelittosiphonia stimpsonii (Harvey) Kudo & Masuda***Vertebrata subulifera* (C.Agardh) Kuntze**

Lectotype (Maggs & Hommersand,

Hutchinsia subulifera C.Agardh

1993): LD 41607

Polysiphonia subulifera (C.Agardh) Harvey

Venice, Italy; undated

***Vertebrata thuyoides* (Harvey) Kuntze**

Lectotype (Maggs & Hommersand,

Polysiphonia thuyoides Harvey

1993): TCD

Boergeseniella thuyoides (Harvey) Kylin

Milltown Malbay, Ireland; 1831

***Vertebrata tripinnata* (J.Agardh) O.Kuntze**Lectotype (Díaz-Tapia *et al.*,*Polysiphonia tripinnata* J.Agardh (1842, p. 142; *Algae maris Mediterranei et Adriatici*, observationes in
diagnosin specierum et dispositionem generum. Apud Fortin, Masson et Cie, Paris)2013b): LD J. Agardh's Herbarium
40938[Kuntze transferred "*Polysiphonia tripinnata* Harvey" to *Vertebrata*, presumably a typographical error as
the basionym is *P. tripinnata* J.Agardh (1842)]

Trieste, Italy

***Vertebrata urbana* (Harvey) Kuntze**

Probable Holotype: TCD 186

Polysiphonia urbana HarveyTable Bay, Cape Province, South
Africa

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.

Table 4. Genus *Melanothamnus* with new combinations resulting from the present study printed in bold, followed by basionyms and taxonomic synonyms.

New combination (if any)	Type material	Notes
Basionym	Type locality, collection date	
Synonyms		
<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) Díaz-Tapia & Maggs, comb. nov.	Holotype: GB Juan Fernández Islands, Chile	Figs 9-18
<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, Uppsala)		

<i>Melanothamnus apiculatus</i> (Hollenberg) Díaz-Tapia & Maggs, comb. nov.	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>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		
<i>Melanothamnus bajacali</i> (Hollenberg) Díaz-Tapia & Maggs, comb. nov.	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>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		
<i>Melanothamnus balianus</i> (D.E.Bustamante, B.Y.Won & T.O.Cho) Díaz-Tapia & Maggs, com. nov.	Holotype: CUK 7937 Blue Lagoon beach, Padang Bai, Karangasem, Bali, Indonesia; 27.iv. 2012.	Molecular data from the type locality (Bustamante <i>et al.</i>, 2013b)
<i>Neosiphonia baliana</i> D.E.Bustamante, B.Y.Won & T.O.Cho (2013 b, pp. 516-518; <i>Neosiphonia baliana</i> sp. nov. and <i>N.</i>		

silvae sp. nov. (Rhodomelaceae, Rhodophyta) from

Bali, Indonesia. *Botanica Marina*, **56**: 515-524)

***Melanothamnus blandii* (Harvey) Díaz-Tapia & Maggs,
comb. nov.**

Polysiphonia blandii Harvey (1862, pl. 184; *Phycologia
australica*.... 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)

***Melanothamnus cheloniae* (Hollenberg & J.N.Norris) Díaz-
Tapia & Maggs, comb. nov.**

Polysiphonia sphaerocarpa var. *cheloniae* Hollenberg &
J.N.Norris (1977, p. 16-17; The red alga *Polysiphonia*
(Rhodomelaceae) in the Northern Gulf of California.

Holotype: US 160602
Sonora, Gulf of California, Mexico;
21.i.1974

Plastid character (Hollenberg & Norris,
1977; fig. 4B)

Smithsonian Contributions to the Marine Sciences, 1: 1-21)

Neosiphonia cheloniae (Hollenberg & J.N.Norris) J.N.Norris

***Melanothamnus collabens* (C.Agardh) Díaz-Tapia & Maggs,
comb. nov.**

Hutchinsia collabens C.Agardh (1824, p. 153; *Systema algarum*.
Berlinginiana, Lundae)

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,
2013)

Polysiphonia collabens (C.Agardh) Kützing

Streblocladia collabens (C.Agardh) Falkenberg

Neosiphonia collabens (C.Agardh) Díaz-Tapia & Bárbara

***Melanothamnus concinnus* (Hollenberg) Díaz-Tapia & Maggs, comb. nov.**

Holotype: US 61210;

La Jolla, California, USA;

26.xii.1936.

Plastid character observed in our study of the type material

Polysiphonia concinna Hollenberg (1944, pp. 474-475; An account of the species of *Polysiphonia* on the Pacific coast of North America. II. *Polysiphonia*. *American Journal of Botany*, 31: 474-483)

Polysiphonia johnstonii var. *concinna* (Hollenberg) Hollenberg

Neosiphonia concinna (Hollenberg) J.N.Norris

***Melanothamnus decumbens* (T.Segi) Díaz-Tapia & Maggs, comb. nov.**

Holotype: SAP 25880;

Mihonoseki, Shimane Prefecture,

Japan; vi.1948.

3-celled carpogonial branches; plastid character (Kim, 2003, fig. 5F). Molecular data available from Korea (Kim & Yang, 2006)

Polysiphonia decumbens T.Segi (1951, p. 218; Systematic study of the genus *Polysiphonia* from Japan and its vicinity. *Journal of the Faculty of Fisheries, Prefectural University of Mie*, 1: 169-272)

Neosiphonia decumbens (T.Segi) M.-S.Kim & I.K.Lee

***Melanothamnus ecorticatus* (R.E.Norris) Díaz-Tapia & Maggs, comb. nov.**

Fernandosiphonia ecorticata R.E.Norris (1994, p. 434; Some cumophytic Rhodomelaceae (Rhodophyta) occurring in Hawaiian surf. *Phycologia* 33: 434-443)

Holotype: BISH 630042

Keokea Bay, Hawai'i; v.1990

Plastid character; ostiolar cells larger than other pericarpial cells (Abbott, 1999)

***Melanothamnus eastwoodiae* (Setchell & N.L.Gardner) Díaz-Tapia & Maggs, comb. nov.**

Polysiphonia eastwoodiae Setchell & N.L.Gardner (1930, p. 161, as *P. eastwoodae*; Marine algae of the Revillagigedo Islands expedition in 1925. *Proceedings of the California Academy of Sciences*, 4: 109-215)

Holotype: CAS 173674

Islas Revillagigedo

Plastid character observed in type material

Neosiphonia eastwoodae (Setchell & N.L.Gardner) Xiang Si-duan

***Melanothamnus ferulaceus* (Suhr ex J.Agardh) Díaz-Tapia & Maggs, comb. nov.**

Type materials are in LD, J.Agardh's Herbarium (not seen)

Plastid character in Panama and Brazil. Molecular data from Panama

<i>Polysiphonia ferulacea</i> Suhr ex J.Agardh (1863, p. 980; <i>Species Genera et Ordines Algarum</i> C.W.K. Glerup, Lundae)	Atlantic Mexico; North America; Guadeloupe; Hawaiian Islands; Marquesas Islands; Australia	(Mamoozadeh & Freshwater, 2012; Guimarães <i>et al.</i> , 2004)
<i>Neosiphonia ferulacea</i> (Suhr ex J.Agardh) S.M.Guimarães & M.T.Fujii		
<i>Melanothamnus fibrillosus</i> (Okamura) Díaz-Tapia & Maggs, comb. nov.	Lectotype (Uwai & Masuda, 1999): SAP	3-celled carpogonial branches, plastid character, cells surrounding the ostiole
<i>Pterosiphonia fibrillosa</i> Okamura (1912, p. 172; <i>Icones of Japanese Algae. Vol. II (10)</i> . Privately published, Tokyo)	Shirahama, Chiba Prefecture, Japan; undated	much larger than the cells below (Uwai & Masuda, 1999, figs. 18, 19).
<i>Kintarosiphonia fibrillosa</i> (Okamura) S. Uwai & Masuda		
<i>Melanothamnus flavimarinus</i> (M.-S.Kim & I.K.Lee) Díaz-Tapia & Maggs, comb. nov.	Holotype: SNU IBA001 Bangpo, Anmyondo, Korea; 17.vii.1988.	3-celled carpogonial branches; plastid character (Kim & Lee, 1999, fig. 5). Molecular data available from the type locality (Kim & Yang, 2006)
<i>Neosiphonia flavimarina</i> M.-S.Kim & 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)		
<i>Melanothamnus forfex</i> (Harvey) Díaz-Tapia & Maggs, comb. nov.	Lectotype (Womersley, 1979): TCD 15353-4	3-celled carpogonial branches; plastid character, molecular data available from

<i>Polysiphonia forfex</i> Harvey (1859, pl. XCVI; <i>Phycologia Australica</i> Vol. 2. Lovell Reeve & Co, London)	Rottnest Island, Western Australia	the type locality (this work)
<i>Melanothamnus gorgoniae</i> (Harvey) Díaz-Tapia & Maggs, comb. nov.	Syntypes: TCD 12801-4, NY 900637-8	3-celled carpogonial branches observed in Brazil (Guimaraes, <i>et al.</i> , 2004);
<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)	Key West, Florida, U.S.A	plastid character observed in type material (this work)
<i>Neosiphonia gorgoniae</i> (Harvey) S.M.Guimarães & M.T.Fujii		
<i>Melanothamnus harlandii</i> (Harvey) Díaz-Tapia & Maggs, comb. nov.	Probable syntypes: TCD 11955, US 56848	3-celled carpogonial branches. Molecular data available from Korea (Kim, 2003;
<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)	Hong Kong	Kim & Yang, 2006)
<i>Neosiphonia harlandii</i> (Harvey) M.S.Kim & I.K.Lee		
<i>Melanothamnus harveyi</i> (Bailey) Díaz-Tapia & Maggs, comb. nov.	Lectotype (Maggs & Hommersand, 1993): TCD 12810	3-celled carpogonial branches (this work); plastid character. Molecular data
<i>Polysiphonia harveyi</i> Bailey (1848, p. 38; <i>Continuation of the</i>	Bailey; Stonington, Connecticut,	available from the type locality (McIvor

- list of localities of algae in the United States. *Proceedings of the American Academy of Arts and Sciences*, 4: 327-335)
- Neosiphonia harveyi* (Bailey) M.-S.Kim, H.-G.Choi, Guiry & G.W.Saunders
- Melanothamnus hawaiiensis* (Hollenberg) Díaz-Tapia & Maggs, comb. nov.**
- Polysiphonia hawaiiensis* Hollenberg (1968 *a*, pp. 66-67; An account of the species of *Polysiphonia* of the central and western tropical Pacific ocean. II *Oligosiphonia*. *Pacific Science*, 22: 56-98)
- Neosiphonia hawaiiensis* (Hollenberg) M.-S.Kim & I.A.Abbott
- Melanothamnus incomptus* (Harvey) Díaz-Tapia & Maggs, comb. nov.**
- Polysiphonia incompta* Harvey (1847, p. 44; *Nereis australis*.... Reeve Brothers, London)
- Melanothamnus japonicus* (Harvey) Díaz-Tapia & Maggs, comb. nov.**
- USA; vii.1847 *et al.*, 2001)
- Holotype: US 48524
Waikiki beach, O'ahu Island,
Hawai'i; 21.i.1963
- 3-celled carpogonial branches (Kim & Abbott, 2006). Plastid character (Abbott, 1999, fig. 122C)
- Probable holotype: TCD 192
False Bay, Cape Province, South
Africa
- Plastid character. Molecular data
available from the type locality (this
work)
- Lectotype (Masuda *et al.*, 1995):
TCD 11905
- Plastid character (this work); 3-celled
carpogonial branches. Molecular data

<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)	Hakodate, Japan; v.1854	available from the type locality (Kim & Yang, 2006)
<i>Neosiphonia japonica</i> (Harvey) M.S.Kim & I.K.Lee		
<i>Melanothamnus johnstonii</i> (Setchell & Gardner) Díaz-Tapia & Maggs, comb. nov.	Holotype: CAS1361 San Esteban Island, Gulf of California; iv.1921	Plastid character. Molecular data available from the type locality (this work). 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 character of having (5-) 6 pericentral
<i>Polysiphonia johnstonii</i> Setchell & Gardner (1924, p. 767; XXIX Expedition of the California Academy of Sciences to the Gulf of California in 1921. The Marine Algae. <i>Proceeding of the California Academy of Science, Series 4</i> 12: 695-949)		
<i>Neosiphonia johnstonii</i> (Setchell & N.L.Gardner) J.N.Norris		

		cells.
<i>Melanothamnus nudus</i> (N.R.Mamoozadeh & D.W.Freshwater) D.W.Freshwater, comb. nov.	Holotype: US 211334	Molecular data available from the type
<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)	Parque de Juventud, Calle Primero, Colon, Caribbean coast of Panama; 20.v.2009	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.	Holotype: CUK 7976	Plastid character. Molecular data
<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)	Lagunillas, Pisco, Ica, southern coast of Lima, Peru; 21.viii.2008	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
<i>Polysiphonia platycarpa</i> Børgesen (1934, p. 23; Some Indian	Bombay, India; 19.xii.1927	character (Iyengar & Balakrishnan, 1949, fig. 1)

Rhodophyceae especially from the shores of the Presidency of Bombay-IV. <i>Bulletin of Miscellaneous Information, Royal Botanic Gardens, Kew</i> , 1934: 1-30)		
<i>Melanothamnus pseudovillum</i> (Hollenberg) Díaz-Tapia & Maggs, comb. nov.	Holotype: US 61232; North Island, Johnston Islands; 22.vi.1965	Cell walls “hyaline” (Hollenberg, 1968 <i>a</i>). Molecular data available from Panama (Mamoozadeh & Freshwater, 2011)
<i>Polysiphonia pseudovillum</i> Hollenberg (1968 <i>a</i> , 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)		
<i>Melanothamnus ramireziae</i> (D.E.Bustamante, B.Y.Won & T.O.Cho) Díaz-Tapia & Maggs, comb. nov.	Holotype: CUK 6511 Lagunillas, Pisco, Ica, Peru; 21.viii.2008.	Plastid character, 3-celled carpogonial branches. Molecular data available from the type locality (Bustamante <i>et al.</i> , 2013 <i>a</i> , fig. 1f)
<i>Neosiphonia ramirezii</i> D.E.Bustamante, B.Y.Won & T.O.Cho (2013 <i>a</i> , <i>Neosiphonia ramirezii</i> sp. nov. (Rhodomelaceae, Rhodophyta) from Peru. <i>Algae</i> , 28: 73-82)		
<i>Melanothamnus silvae</i> (D.E.Bustamante, B.Y.Won & T.O.Cho) Díaz-Tapia & Maggs, comb. nov.	Holotype: CUK 7976 Geger, Nusadua, Bali, Indonesia; 26.iv.2012	Plastid character. Molecular data available from the type locality (Bustamante <i>et al.</i> , 2013 <i>b</i> , figs 22-23)
<i>Neosiphonia silvae</i> D.E.Bustamante, B.Y.Won & T.O.Cho		

(2013b, pp. 518-520; *Neosiphonia baliana* sp. nov. and *N. silvae* sp. nov. (Rhodomelaceae, Rhodophyta) from Bali, Indonesia. *Botanica Marina*, 56: 515-524)

***Melanothamnus simplex* (Hollenberg) Díaz-Tapia & Maggs, comb. nov.**

Polysiphonia simplex Hollenberg, (1942, p. 782; An account of the species of *Polysiphonia* on the Pacific coast of North America. I. Oligosiphonia. *American Journal of Botany*, 29: 772-785)

Neosiphonia simplex (Hollenberg) Y.-P.Lee

***Melanothamnus sphaerocarpus* (Børgesen) Díaz-Tapia & Maggs, comb. nov.**

Polysiphonia sphaerocarpa Børgesen (1918, p. 271; The marine algae of the Danish West Indies. Part 3. Rhodophyceae (4). *Dansk Botanisk Arkiv*, 3: 241-304)

Neosiphonia sphaerocarpa (Børgesen) M.-S.Kim & I.K.Lee

***Melanothamnus strictissimus* (J.D.Hooker & Harvey) Díaz-**

Holotype: US 61238

Laguna Beach, Orange County, California, U.S.A; 14.v.1937

Isotypes: US , C

Store Nordsidebugt, St. Thomas, Virgin Islands

Probable syntype: BM 561312

Plastid character. Molecular data available from the type locality (this work).

RbcL sequence not included in our phylogeny because it is only 1% divergent from *N. ramirezii*.

Plastid character. Molecular data available from Florida (Mamoozadeh & Freshwater, 2011, fig. 18)

Plastid character (this work). Molecular

Tapia & Maggs, comb. nov.	New Zealand	data available from the type locality
<i>Polysiphonia strictissima</i> J.D.Hooker & Harvey (1845, p. 538; Algae Novae Zelandiae.... <i>London Journal of Botany</i> , 4: 521- 551)		(Stuercke & Freshwater, 2010)
<i>Melanothamnus thailandicus</i> (N.Muangmai & C.Kaewsuralikhit) Díaz-Tapia & Maggs, comb. nov.	Holotype: KUMF-SRC 03-011-1	3-celled carpogonial branches. Molecular
<i>Neosiphonia thailandica</i> N.Muangmai & 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)	Sri Racha Harbor, Chon Buri, Thailand; 11.iii.2011	data available from the type locality (Muangmai <i>et al.</i> , 2014)
<i>Melanothamnus yongpilaii</i> (B.Kim & M.-S.Kim) Díaz-Tapia & Maggs, comb. nov.	Holotype: JNUB 140704-101	3-celled carpogonial branches; plastid
<i>Neosiphonia yongpilaii</i> B.Kim & M.-S.Kim (2016, pp. 324-325; <i>Neosiphonia yongpilaii</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)	Jongdal, Jeju Island, Korea; 04.iv.2014	character. Molecular data available from the type locality (Kim & Kim, 2016, fig. 14)

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).

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. They are printed in bold, followed by basionyms and taxonomic synonyms.

Binomial in <i>Melanothamnus</i> (if any)	Type material	Notes
Basionym	Type locality	
Synonyms		
<i>Melanothamnus hancockii</i> (E.Y.Dawson) Díaz-Tapia & Maggs, comb. nov.	Holotype: LAM EYD629c Baja California, Mexico; 16.ii.1940	Plastid character. Molecular data from Japan (this work)
<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> (E.Y.Dawson) R.E.Norris		
<i>Melanothamnus masonii</i> (Setchell & N.L.Gardner) Díaz-Tapia & Maggs, comb. nov.	Holotype: CAS 173618 Isla Guadalupe, México; iv.1925	

Polysiphonia masonii Setchell & Gardner (1930, p. 160; Marine algae of the Revillagigedo Islands expedition in 1925.

Proceedings of the California Academy of Sciences, 4: 109-215)

Neosiphonia masonii (Setchell & N.L.Gardner) J.N.Norris

***Melanothamnus minutissimus* (Hollenberg) Díaz-Tapia & Maggs, comb. nov.**

Holotype: US 66797

Plastid character. Molecular data from Japan (this work)

Punta Banda, Baja California,

Polysiphonia minutissima Hollenberg (1942, p. 781, An account of the species of *Polysiphonia* on the Pacific coast of North America. I. Oligosiphonia. *American Journal of Botany*, 29: 772-785)

Mexico; 17.xii.1938

***Melanothamnus nanus* (A.J.K.Millar) Díaz-Tapia & Maggs, comb. nov**

Holotype: MELU AM752

Coffs Harbour, New South Wales;

Fernandosiphonia nana A.J.K.Millar (1990, p. 439; Marine red algae of the Coffs Harbour region, northern New South Wales. *Australian Systematic Botany*, 3: 293-593)

27.viii.1980

Melanothamnus notoensis (Segi) Díaz-Tapia & Maggs, comb.

Holotype: SAP 025894

Plastid character in Korea (Nam & Kang,

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

Faculty of Fisheries, Prefectural University of Mie, 1: 169-272)

Neosiphonia porrecta (Segi) Y.-P. Lee

***Melanothamnus savatieri* (Hariot) Díaz-Tapia & Maggs, comb. nov.**

Lectotype (Kim, 2005): PC
0011879

3-celled carpogonial branches in
Malaysia (Masuda *et al.*, 2001).

Polysiphonia savatieri Hariot (1891, p. 226; Liste des algues
marines rapportés de Yokoska (Japon) par M. le Dr Savatier.

Yokosuka, Kanagawa Prefecture,
Japan

Molecular data available from Korea
(Phillips *et al.*, 2000)

*Mémoires de la Société nationale des sciences naturelles de
Cherbourg, 27: 211-230)*

Neosiphonia savatieri (Hariot) M.S.Kim & I.K.Lee

***Melanothamnus sparsus* (Setchell) Díaz-Tapia & Maggs, comb. nov.**

Holotype: UC 261144;
Arue Reef, Tahiti; 27.vi.1922

Plastid character in Vietnam (Abbott *et al.*, 2002; fig. 27)

Lophosiphonia sparsa Setchell (1926, p. 103; Tahitian algae
collected by W.A. Setchell, C.B. Setchell and H.E. Parks.

University of California Publications in Botany, 12: 61-142)

Polysiphonia sparsa (Setchell) Hollenberg

Neosiphonia sparsa (Setchell) I.A.Abbott

***Melanothamnus teradomariensis* (M.Noda) Díaz-Tapia &**

Holotype: Herbarium Niigata

Molecular data available from Korea

Maggs, comb. nov.	University	(Bárbara <i>et al.</i> , 2013)
<i>Polysiphonia teradomariensis</i> M.Noda (in Noda, M. & 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)	Echigo Province, Japan; 28.xi.1968	
<i>Polysiphonia japonica</i> var. <i>teradomariensis</i> (M.Noda) H.Y.Yoon		
<i>Neosiphonia teradomariensis</i> (M.Noda) M.-S.Kim & I.K.Lee		
<i>Melanothamnus tongatensis</i> (Harvey ex Kützing) Díaz-Tapia & Maggs, comb. nov.	Holotype: L 4083619 Tonga, Friendly Islands; undated	Molecular data available from Panama (Mamoozadeh & Freshwater, 2011)
<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)		
<i>Neosiphonia tongatensis</i> (Harvey ex Kützing) M.-S.Kim & I.K.Lee		
<i>Melanothamnus upolensis</i> (Grunow) Díaz-Tapia & Maggs, comb. nov.	Syntypes: W Upolu, Western Samoa	Molecular data available from Hawaii (Sherwood <i>et al.</i> , 2010)

Polysiphonia upolensis Grunow (1874, p. 49; Algen der Fidschi-,

Tonga- und Samoa-Inseln, gesammelt von Dr. E. Graeffe.

Journal des Museum Godeffroy, 3: 23-50)

Neosiphonia upolensis (Grunow) M.S.Kim & Boo

***Melanothamnus yendoi* (T.Segi) Díaz-Tapia & Maggs, comb. nov.**

Holotype: SAP 0258883

Molecular data available from Korea

Muroran, Hokkaido, Japan;

(Bárbara *et al.*, 2013)

30.iv.1935

Polysiphonia yendoi Segi (1951, p. 211; Systematic study of the genus *Polysiphonia* from Japan and its vicinity. *Journal of the Faculty of Fisheries, Prefectural University of Mie*, 1: 169-272)

Neosiphonia yendoi (Segi) M.-S.Kim & I.K.Lee

Neosiphonia saccorhiza (F.S.Collins & Hervey) J.M.C.Nunes & S.M.Guimarães, nom. inval.

Isotypes: NY, Collins Herbarium

Transfer to *Melanothamnus* is not made

Gibbet Island, Bermuda

here as *N. saccorhiza* is an invalid

Lophosiphonia saccorhiza F.S.Collins & Hervey

combination (the basionym was not

Polysiphonia saccorhiza (F.S.Collins & Hervey) Hollenberg

cited), and the phylogenetic affinities of

Lophosiphonia saccorhiza are unknown.

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 μm ; Fig. 7, 200 μm ; Fig. 8, 100 μm .

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 μm ; Figs 12, 14, 17 and 18, 100 μm ; Figs 13 and 15, 40 μm ; Fig. 16, 20 μm .

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 μm ; Fig. 24, 500 μm .

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 μm ; Figs 26, 28 and 30, 800 μm ; Figs 31, 32, 34, 35 and 37, 100 μm ; Fig. 33, 300 μm ; Fig. 36, 50 μm .

Figs 40-46. Trichoblast nuclei (arrows) in the Polysiphonieae. 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 µm, Fig. 44, 30 µm; Fig. 45, 20 µm; Fig. 46, 100 µm.

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. fucooides* (**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 µm. Arrows show the apical sterile cells and arrowheads the sterile branch of fertile trichoblasts.

Figs 53-58. Carpogonial branches in the Polysiphonieae. 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 carpogonial branches. Scale bars: Fig. 53, 30 µm; Figs 54-58, 20 µm.

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), *Streblacladia 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 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 .

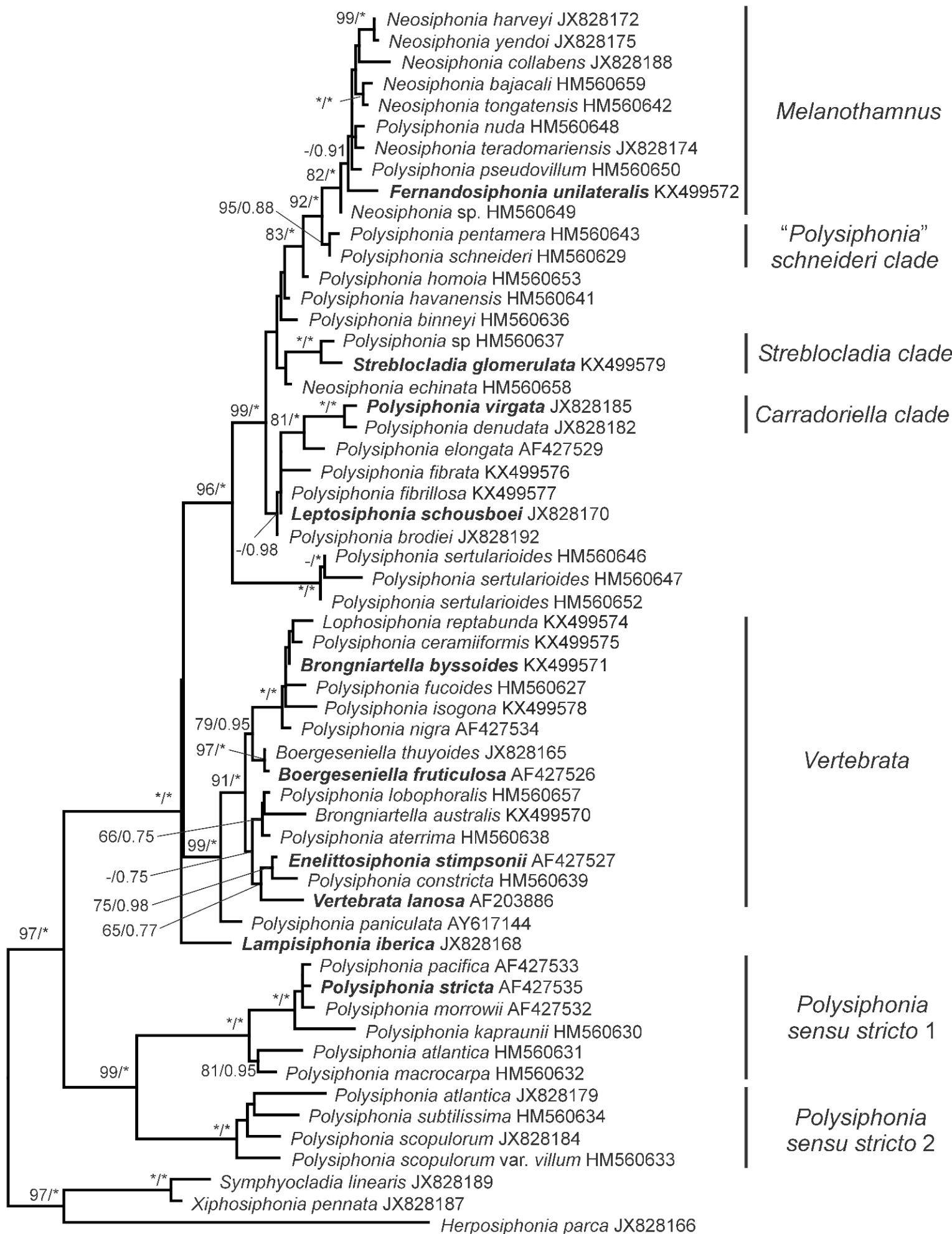
Figs 71-76. Tetrasporangia in the Polysiphonieae. Forming long straight series in *Polysiphonia stricta* (**Fig. 71**, *Polysiphonia sensu stricto* clade 1). Forming spiral series in *Vetebrata lanosa* (**Fig. 72**, *Vertebrata* clade), *Polysiphonia* sp. (**Fig. 74**, *Streblocladia* clade) and *Neosiphonia 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 .

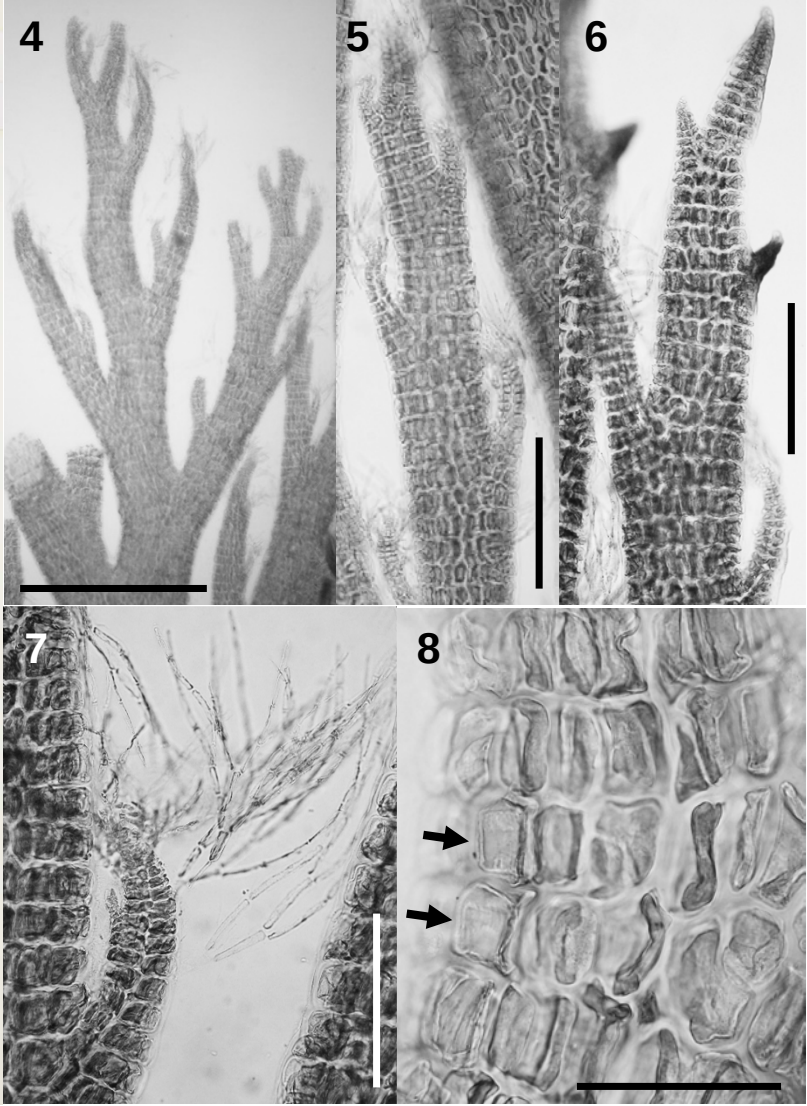
Fig. 77. World map representing the proportion of *Fernandosiphonia* (black) and other Polysiphonieae (grey) species in selected regions where the Polysiphonieae were studied in detail. Data were obtained from the following references after updating the species names: Alaska: Lindstrom (<http://www.seaweedssofaraska.com>);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

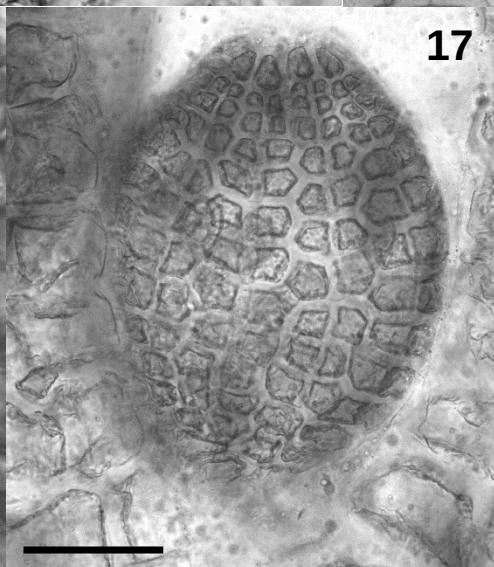
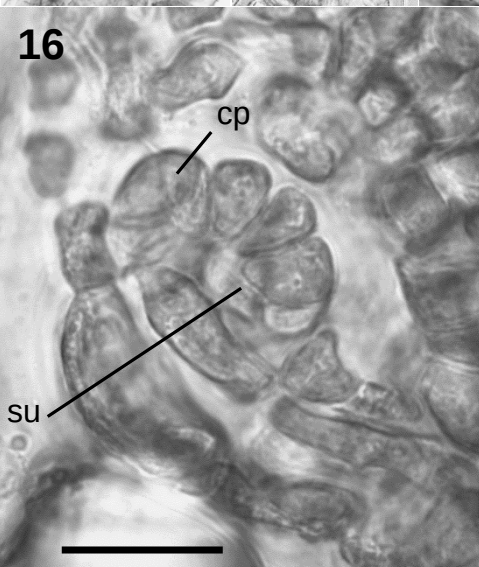
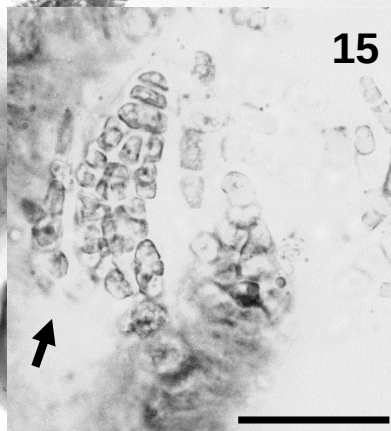
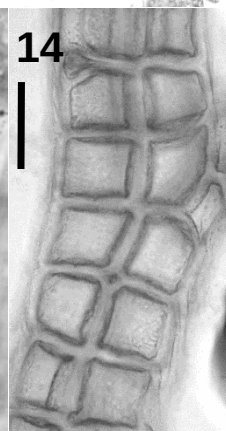
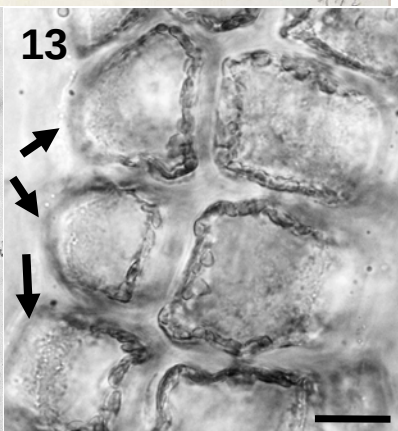
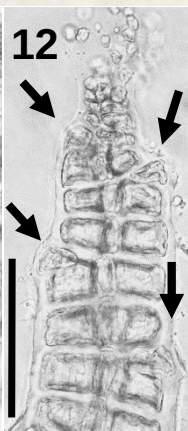
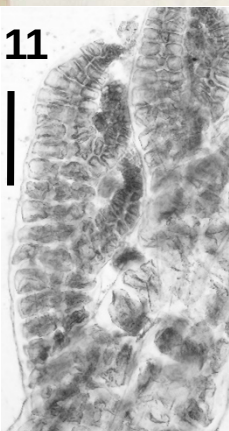
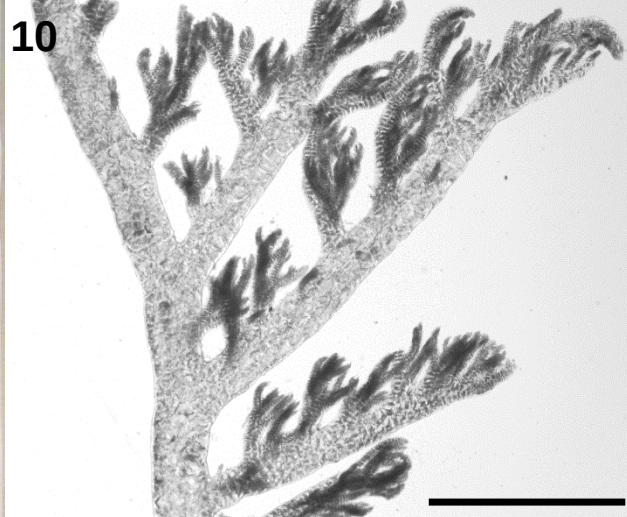
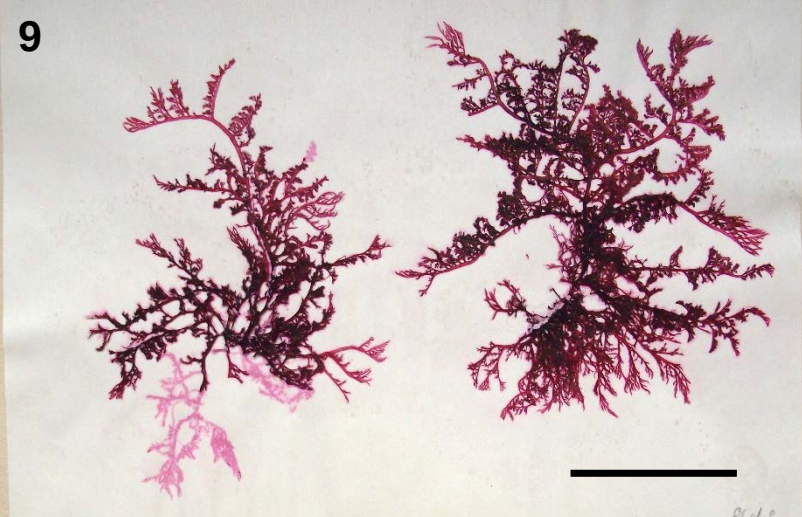
(1998); Korea: Nam & Kang (2012); Panama: Mamoozadeh & Freshwater (2012); Spain (Galicia): Bárbara *et al.* (2005); British Isles: Maggs & Hommersand (1993).

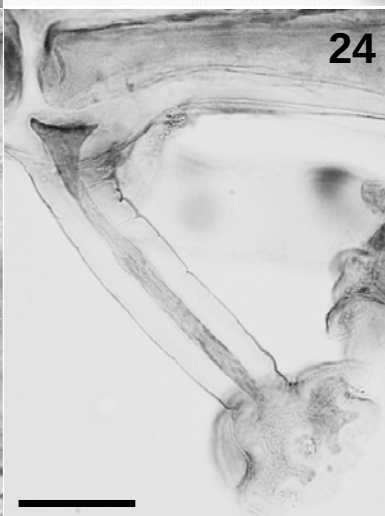
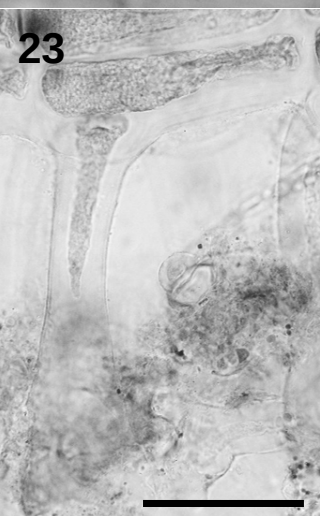
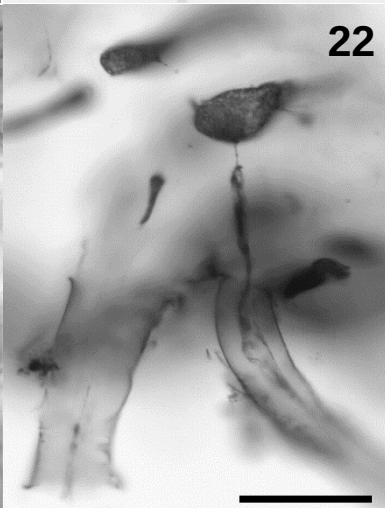
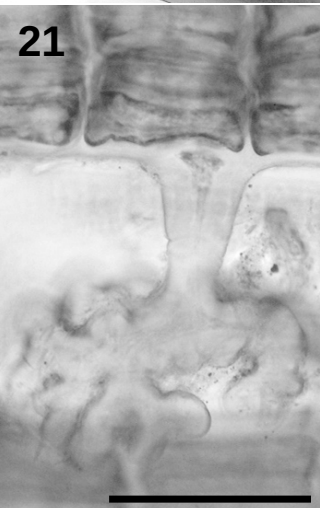
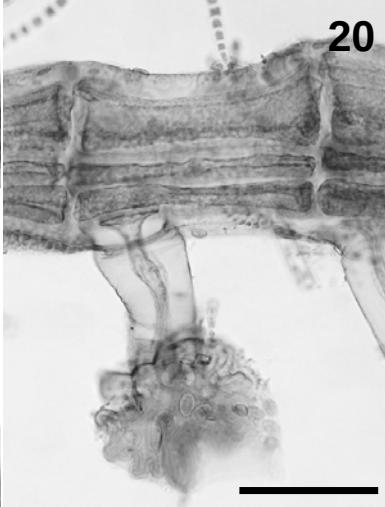
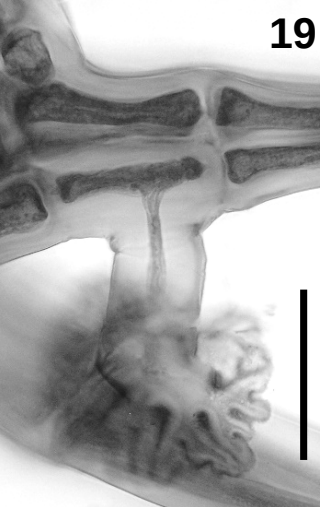
Fig. S1. Chronogram resulting from the Bayesian relaxed molecular clock analysis performed with BEAST.

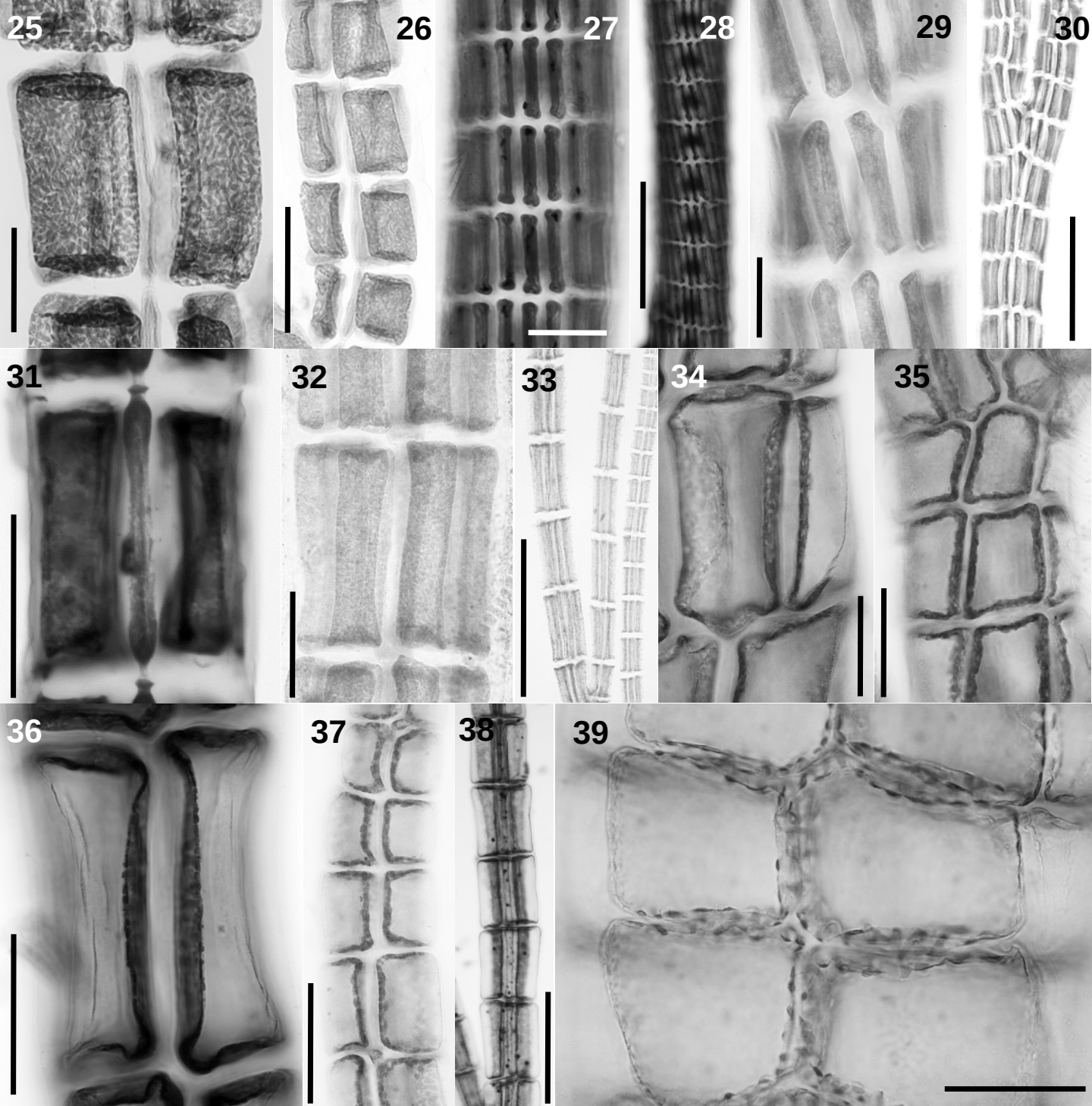
Fig. S2. Chronogram resulting from the autocorrelated molecular clock analysis performed with PhyloBayes.



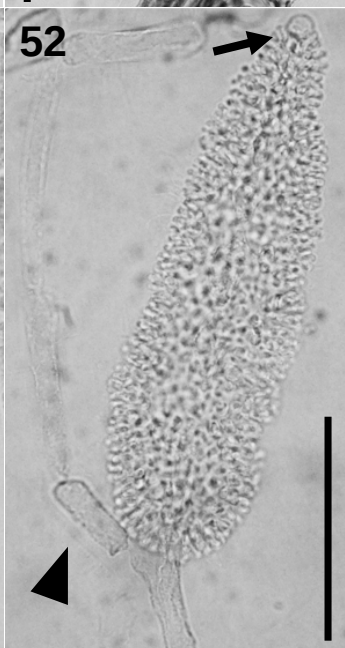
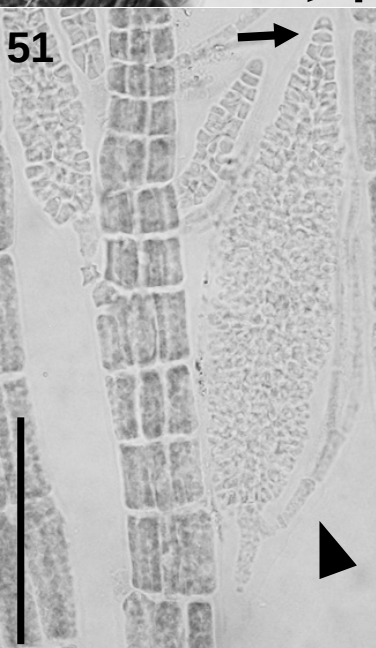
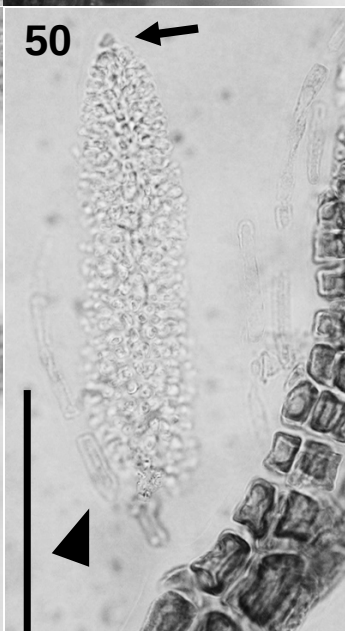
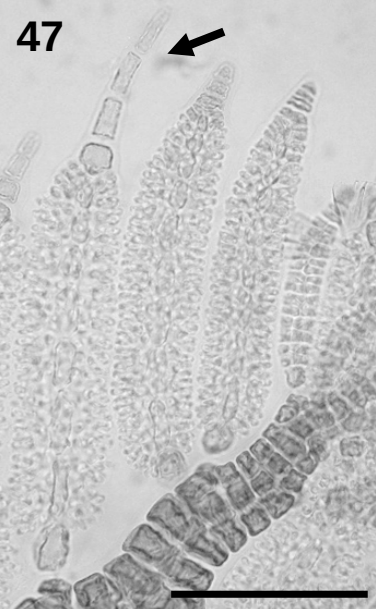


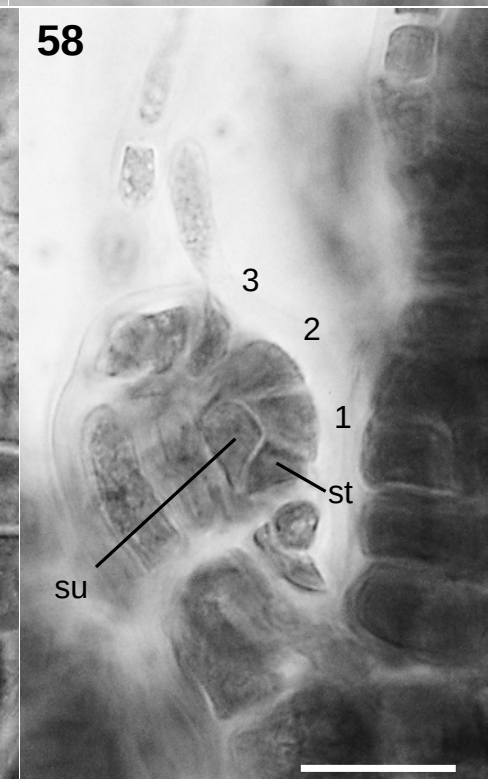
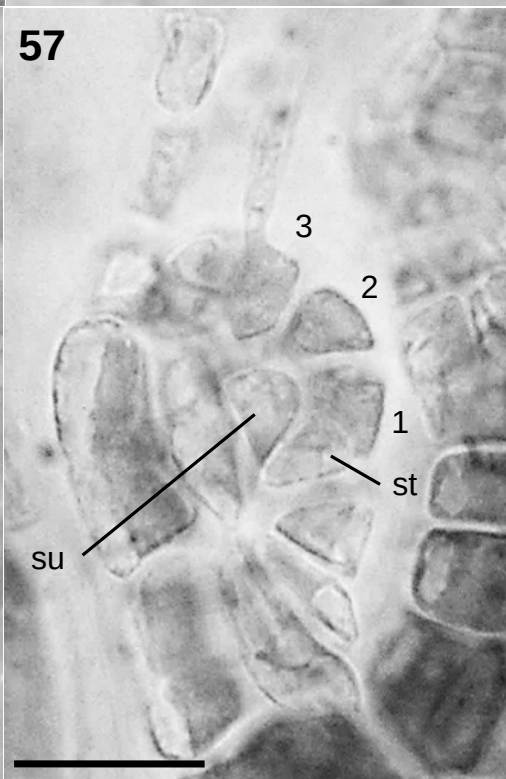
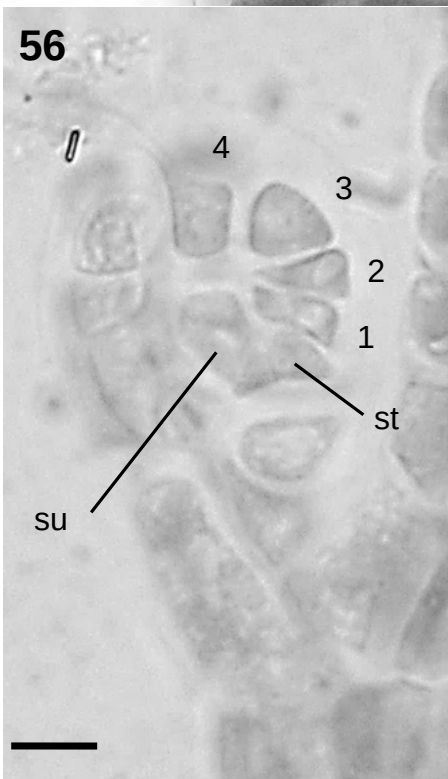
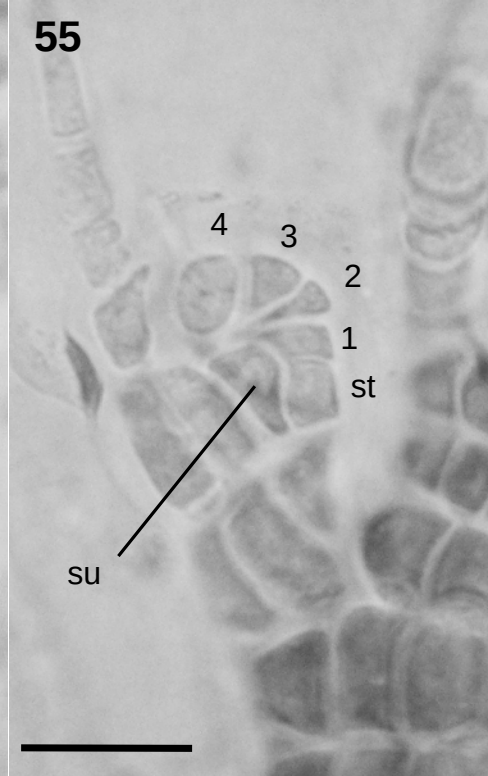
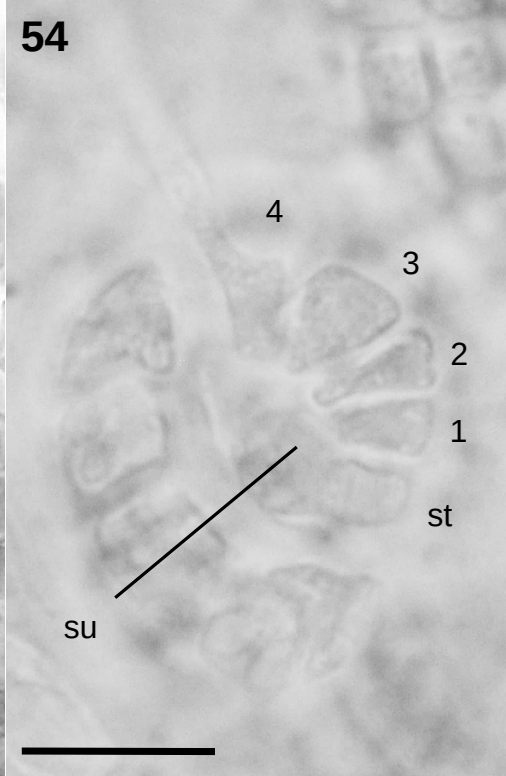
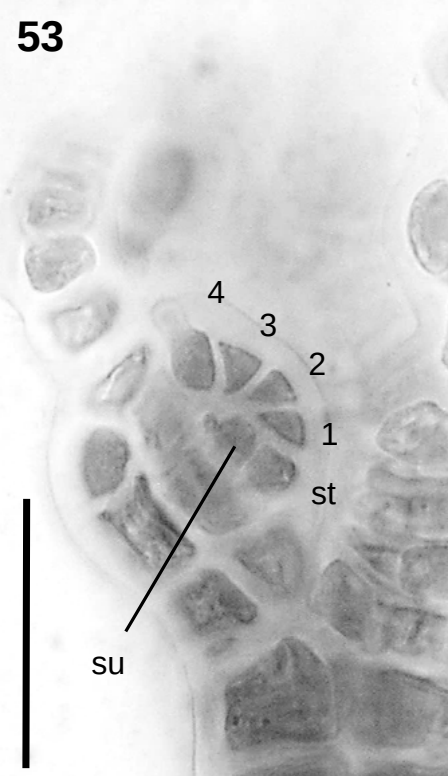


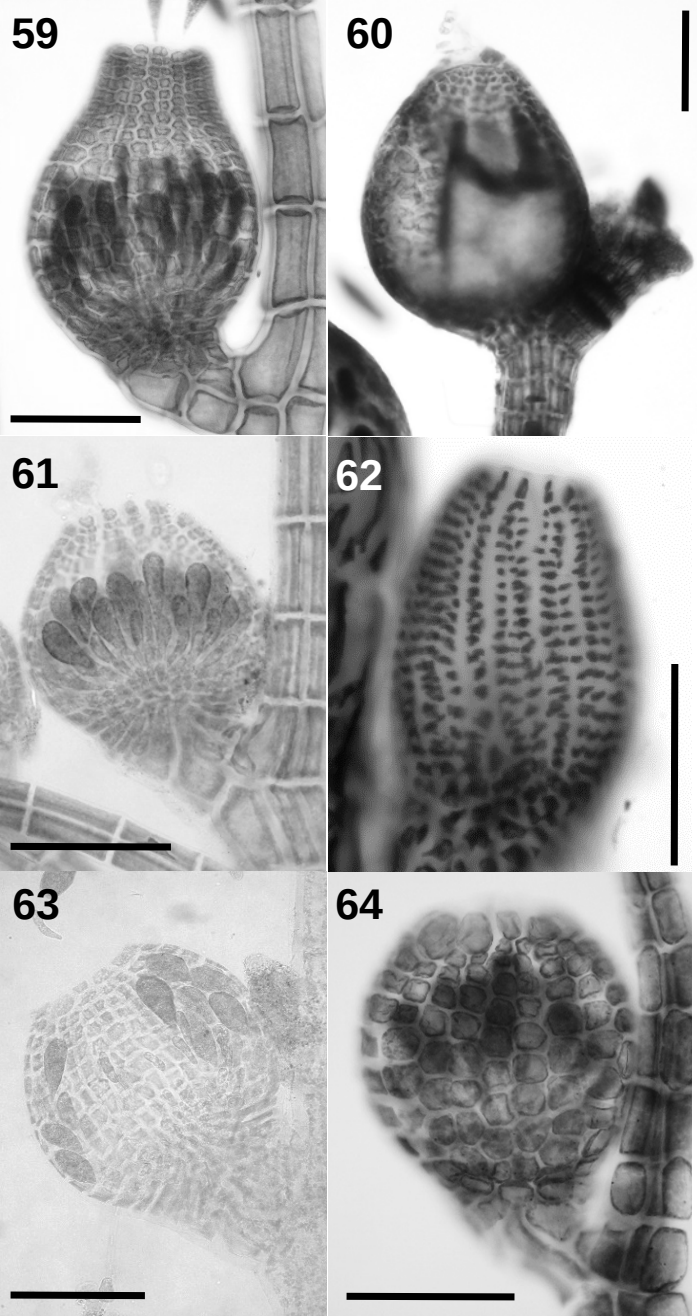


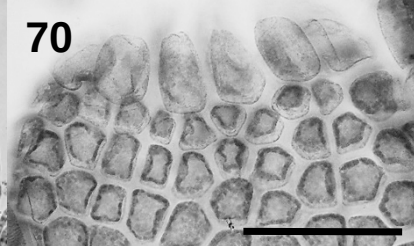
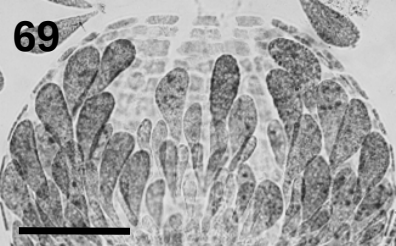
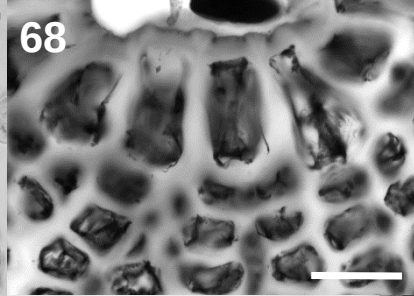
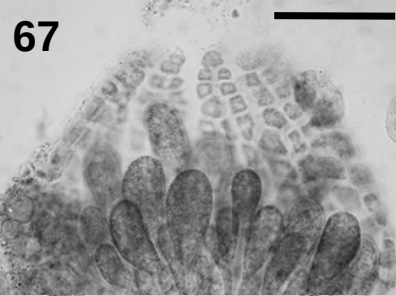
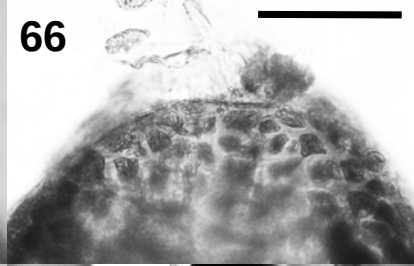
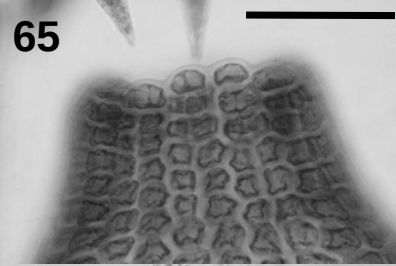


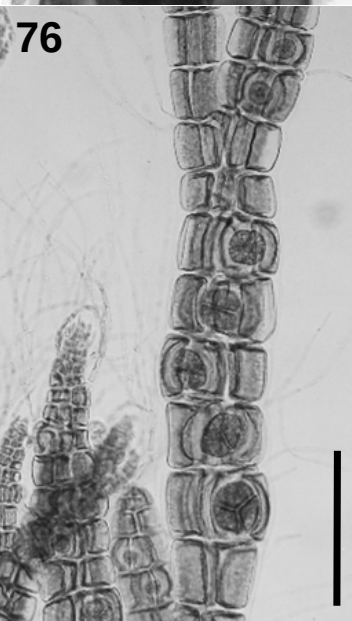
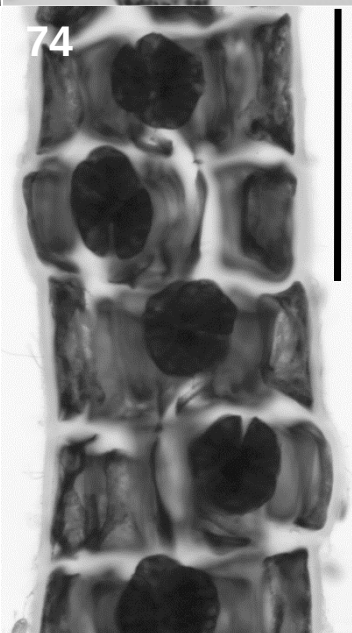
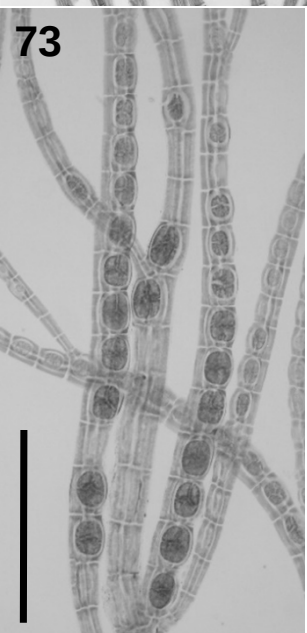
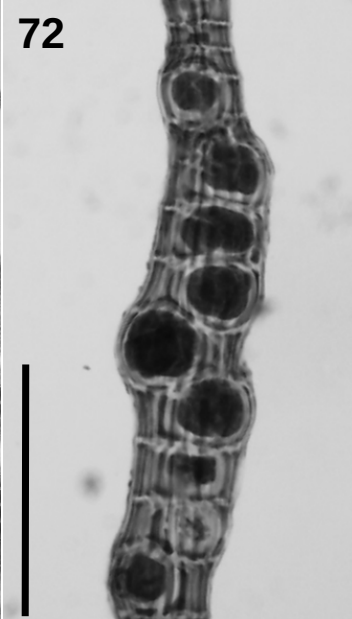












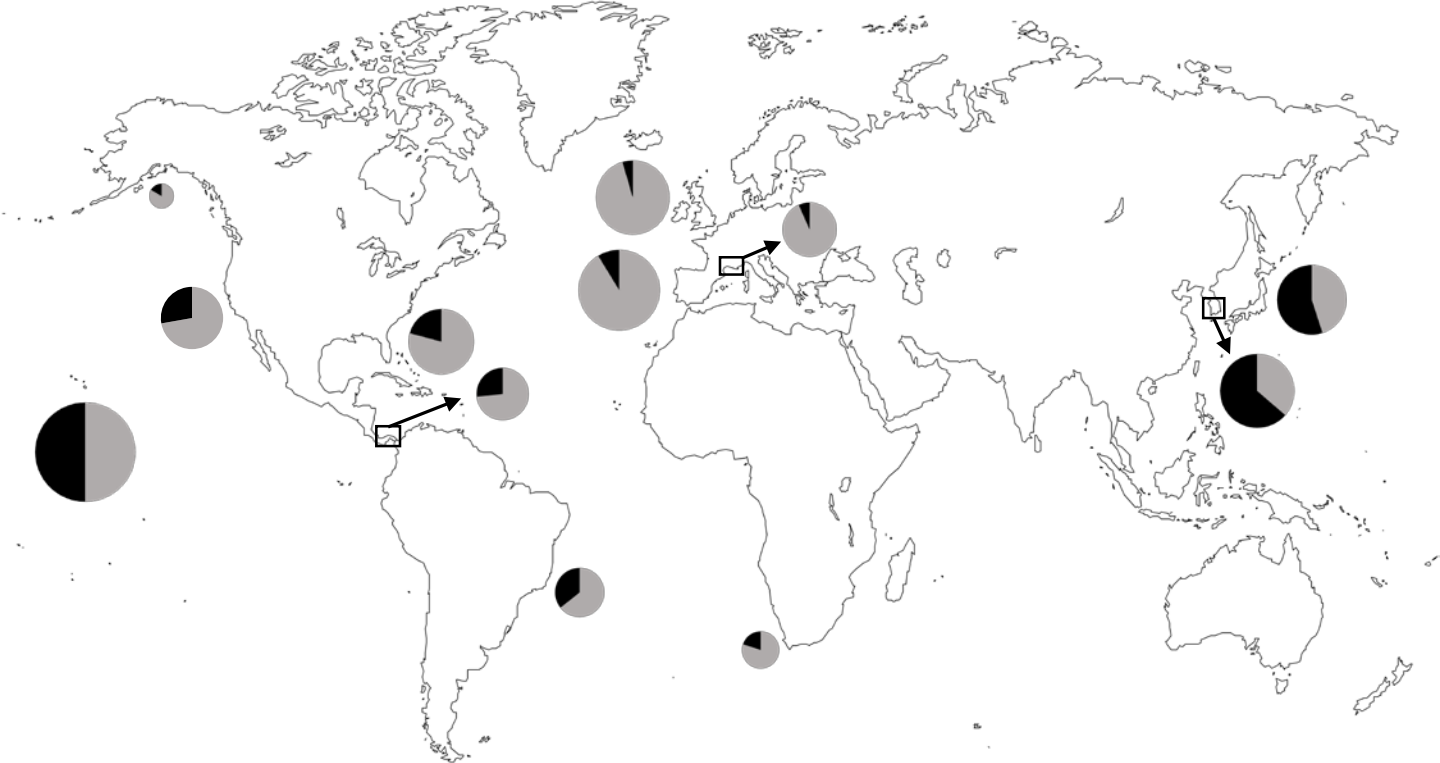


Table S1. Sample information for the species included in the phylogenetic analysis.

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) 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

<i>Neosiphonia ferulacea</i> (Suhr ex J.Agardh) S.M.Guimarães & M.T.Fujii	Mamoozadeh & Freshwater (2011)	HM573584	-
<i>Neosiphonia flavimarina</i> M.-S.Kim & I.K.Lee	Kim & Yang (2006)	DQ787481	-
<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
<i>Neosiphonia peruviansis</i> D.E.Bustamante, B.Y.Won, M.E.Ramírez & T.O.Cho	Bustamante <i>et al.</i> (2012b)	JN989969	-
<i>Neosiphonia</i> cf. <i>savatieri</i> (Hariat) M.S.Kim & I.K.Lee	Onno, Okinawa, Japan, 10.xi.2003, C. Trowbridge; BM	KX499558	
<i>Neosiphonia silvae</i> D.E.Bustamante, B.Y.Won & T.O.Cho	Bustamante <i>et al.</i> (2013)	KF146878	-
<i>Neosiphonia ramireziae</i> D.E.Bustamante, B.Y.Won & T.O.Cho	Bustamante <i>et al.</i> (2012a)	KC493352	-
<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 Kützinger) 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 aterrima</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) Greville 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</i> cf. <i>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</i> cf. <i>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 sabulosia</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	Mamoozadeh & Freshwater (2011)	HM573548	HM560646
<i>Polysiphonia sertularioides</i> (Grateloup) J.Agardh	Mamoozadeh & Freshwater (2011)	HM573547	HM560652
<i>Polysiphonia sertularioides</i> (Grateloup) J.Agardh	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.	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>Streblocladia 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

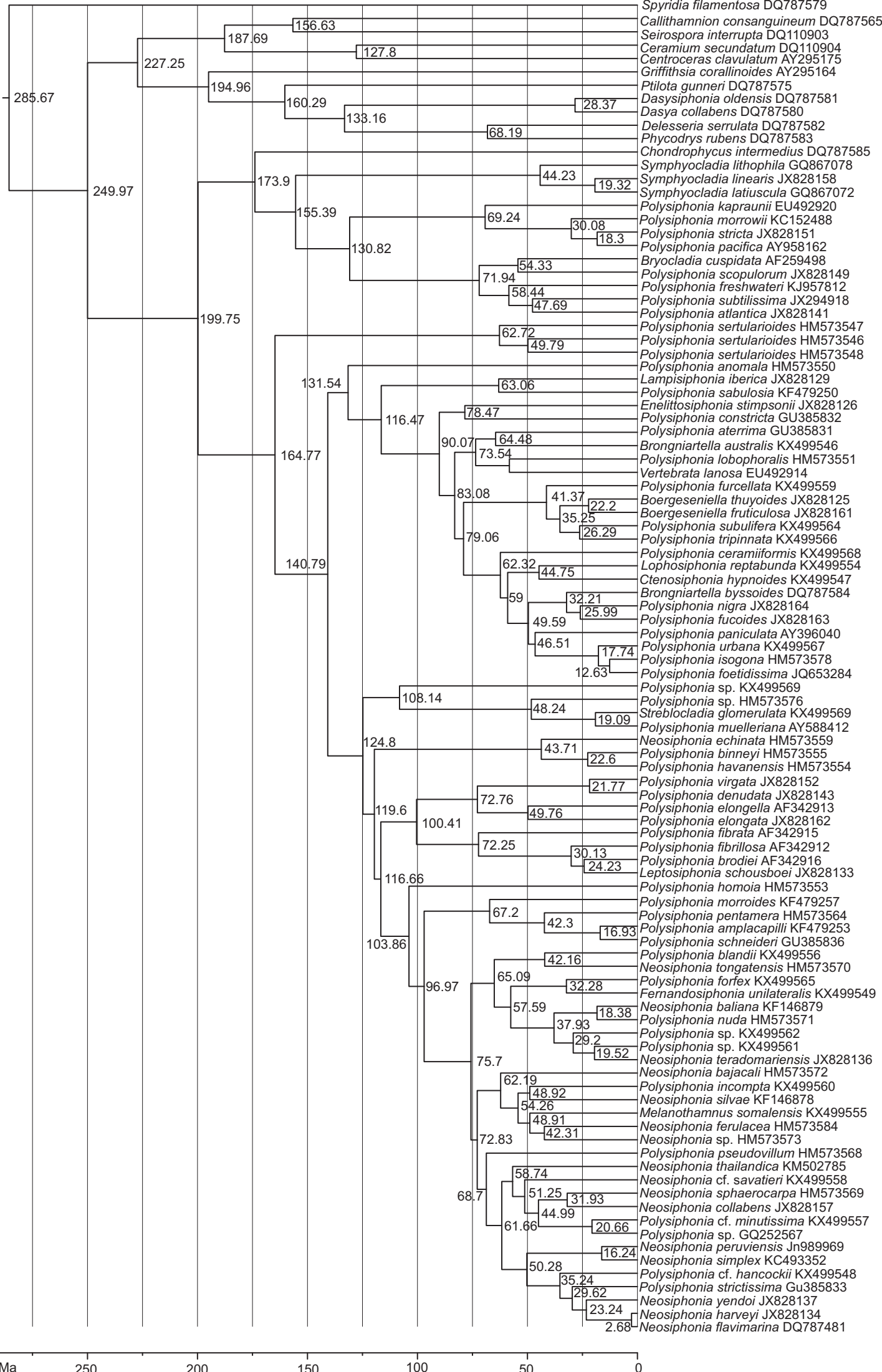
Species	Herbarium	Code
<i>Lophosiphonia mexicana</i> E.Y.Dawson	US	EYD430 (66781)
<i>Polysiphonia beaudettei</i> Hollenberg	US	EYD21379 (5219)
<i>Polysiphonia concinna</i> Hollenberg	US	GJH2015 (61210)
<i>Polysiphonia eastwoodae</i> Setchell & N.L.Gardner	US	55 (66788)
<i>Polysiphonia gorgoniae</i> Harvey	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</i> sp.	<i>Neosiphonia silvae</i>	<i>Neosiphonia ferulacea</i>	<i>Polysiphonia</i> sp.	<i>Polysiphonia</i> cf. <i>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</i> (as <i>ramirezii</i>)	<i>Neosiphonia simplex</i>	<i>Polysiphonia forfex</i>	<i>Fernandosiphonia unilateralis</i>	<i>Melanothamnus afaqhusainii</i>	<i>Melanothamnus somalensis</i>	<i>Fernandosiphonia</i> cf. <i>hancockii</i>	<i>Polysiphonia strictissima</i>	<i>Neosiphonia yendoi</i>	<i>Polysiphonia</i> sp.	<i>Neosiphonia baliana</i>	<i>Polysiphonia</i> sp.	<i>Polysiphonia nuda</i>	<i>Polysiphonia incompta</i>	<i>Neosiphonia teradomariensis</i>
<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	
<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	92.4	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	
<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	
<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	
<i>Neosiphonia</i> sp.	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	
<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	
<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	
<i>Polysiphonia</i> sp.	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	
<i>Polysiphonia</i> cf. <i>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	
<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	
<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	
<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	
<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	
<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	
<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	
<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	
<i>Neosiphonia simplex</i> (as <i>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	
<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	
<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	
<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	
<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	
<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	
<i>Fernandosiphonia</i> cf. <i>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	
<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	
<i>Neosiphonia yendoi</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	
<i>Polysiphonia</i> sp.	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	
<i>Neosiphonia baliana</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	
<i>Polysiphonia</i> sp.	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	
<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	
<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	
<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	

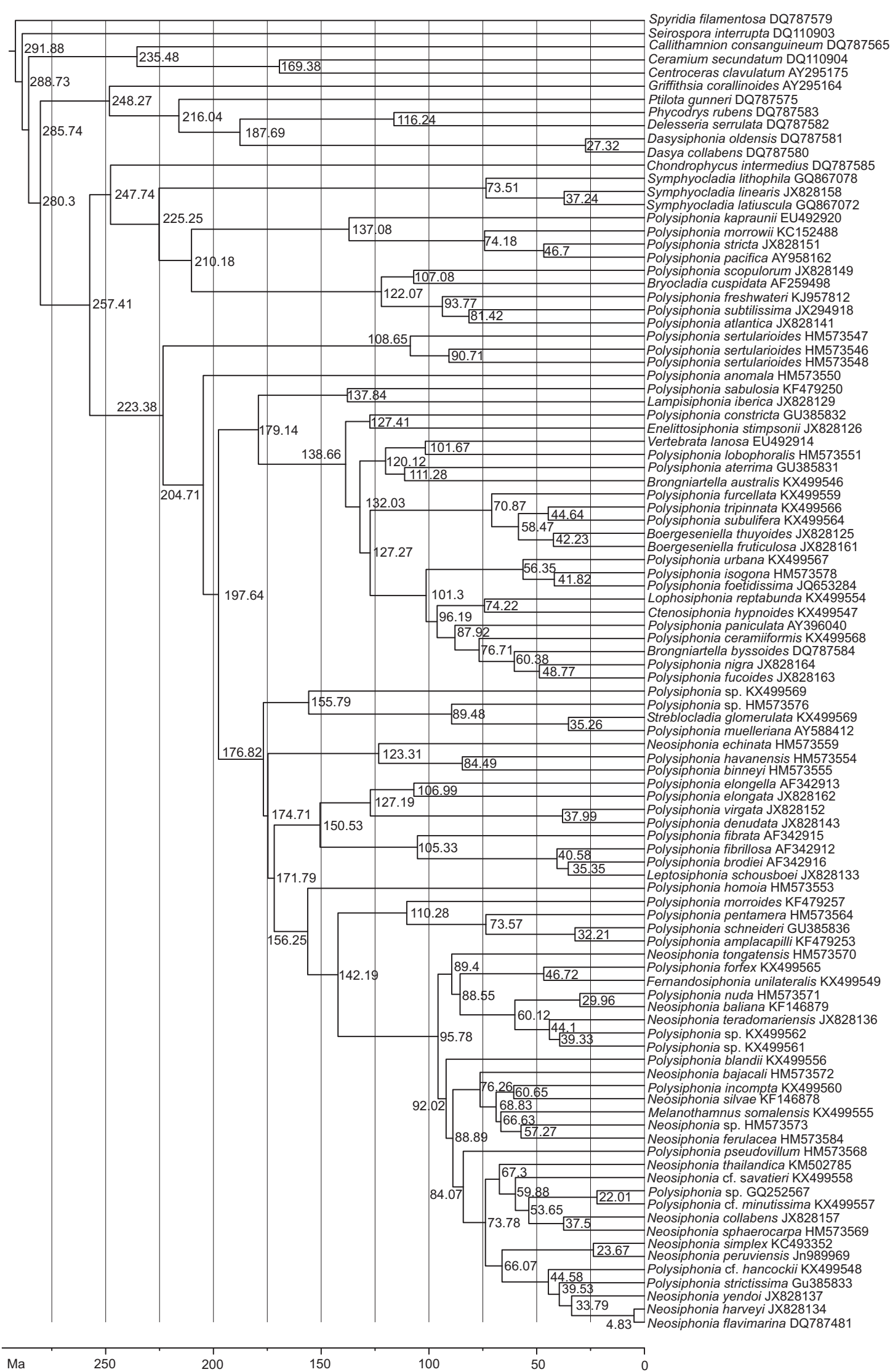
Table S4. Percentage of bases that differ (down) and are identical (above) for the species sequences of the *Vertebrata* clade included in our *rbcL* alignment.

	<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 fucoides</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>Polysphonia 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 fucoides</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