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Photograph of *Ceramium diaphanum* sensu Harvey taken by Christine A. Maggs collected in Mulroy Bay, Donegal, Ireland, epiphytic on *Codium*.

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# Phylogenetic analysis of the red algal tribe Ceramieae reveals multiple morphological homoplasies but defines new genera

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## ABSTRACT

Despite the importance of morphological characters for classification, molecular data are now more widely used than morphology in phylogenetic reconstructions, particularly in studies of algae. The tribe Ceramieae C.Agardh ex Greville (Ceramiaceae) is a widespread, speciose, and morphologically diverse group of valuable red algae with many identified bioactives. We aimed to elucidate phylogenetic relationships in the tribe to delimit genera and provide a new classification. Generic delimitation is currently based on morphological characters, and there has been no overall reassessment of generic circumscriptions and evolutionary relationships using molecular data. We used three molecular markers (mitochondrial COI-5P, plastid *rbcl* and nuclear LSU). Within the Ceramieae, several clades are recovered, although the relationships among major clades are not supported. These clades are here recognized as genera, with new circumscriptions for *Ceramium* Roth, *Carpoblepharis* Kützing, *Herpochondria* F.Schmitz & Falkenberg, *Campylaephora* J.Agardh and *Celeceras* Kützing, and the proposal of *Pseudoceramium* Barros-Barreto & Maggs, gen. nov., *Yoneshigunea* Barros-Barreto, Maggs & M.A.Jaramillo, gen. nov. and *Stirkia* Barros-Barreto & Maggs, gen. nov. The Ceramieae show a high degree of morphological homoplasy among species as well as extreme phenotypic plasticity within species. Genera lack unique synapomorphies and multiple morphological characters are required to define most of them. Molecular data are critical for understanding systematics in this group.

## KEY WORDS

Rhodophyta,  
Ceramieae,  
molecular systematics,  
lectotypification,  
new status,  
new combinations,  
new species,  
new genera.



## RÉSUMÉ

*L'analyse phylogénétique de la tribu des algues rouges Ceramieae révèle de multiples homoplasies morphologiques mais définit de nouveaux genres.*

Malgré l'importance des caractères morphologiques dans la classification, les données moléculaires sont désormais plus largement utilisées que la morphologie dans les reconstructions phylogénétiques, en particulier dans les études sur les algues. La tribu Ceramieae C.Agardh ex Greville (Ceramiales) est un groupe répandu, spécifique et morphologiquement diversifié d'algues rouges d'intérêt avec de nombreux bioactifs identifiés. Nous avons cherché à élucider les relations phylogénétiques dans la tribu pour délimiter les genres et fournir une nouvelle classification. La délimitation générique est actuellement basée sur des caractères morphologiques, et il n'y a pas eu de réévaluation globale des circonscriptions génériques et des relations évolutives à l'aide de données moléculaires. Nous avons utilisé trois marqueurs moléculaires (COI-5P mitochondrial, *rbcL* chloroplastique et LSU nucléaire). Au sein des Ceramieae, plusieurs clades sont reconnus, bien que les relations entre les principaux clades ne soient pas résolues. Ces clades sont ici reconnus comme des genres, avec de nouvelles circonscriptions pour *Ceramium* Roth, *Carpoblepharis* Kützinger, *Herpochondria* F.Schmitz & Falkenberg, *Campylaephora* J.Agardh et *Celeceras* Kützinger, et la proposition de *Pseudoceramium* Barros-Barreto & Maggs, gen. nov., *Yoneshiguea* Barros-Barreto, Maggs & M.A.Jaramillo, gen. nov. et *Stirkia* Barros-Barreto & Maggs, gen. nov. Les Ceramieae montrent un degré élevé d'homoplasie morphologique entre les espèces ainsi qu'une plasticité phénotypique extrême au sein des espèces. Les genres manquent de synapomorphies uniques et plusieurs caractères morphologiques sont nécessaires pour définir la plupart d'entre eux. Les données moléculaires sont essentielles pour comprendre la systématique dans ce groupe.

## MOTS CLÉS

Rhodophyta,  
Ceramiales,  
systématique moléculaire,  
lectotypification,  
statut nouveau,  
combinaisons nouvelles,  
espèce nouvelle,  
genres nouveaux.

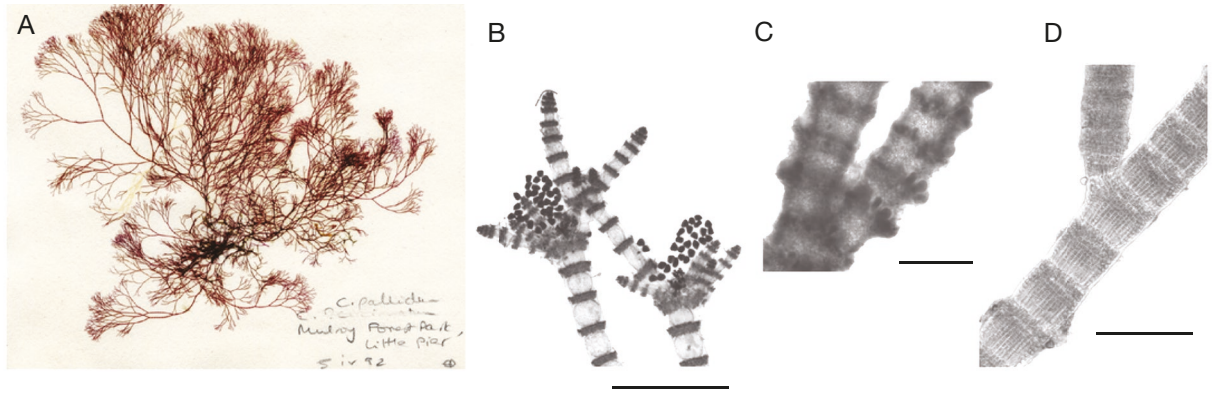
## INTRODUCTION

The red algae have seen dramatic changes in classification at the family and ordinal levels over the last three decades, based mostly on the increasing use of molecular tools (Verbruggen *et al.* 2010; Yoon *et al.* 2010; Saunders *et al.* 2016; Díaz-Tapia *et al.* 2017, 2019). Due to their extraordinary morphological plasticity and ancient origins, the red algae can be seen as a model system for exploring the challenges of reconciling morphological systematics with molecular phylogenies. Sometimes the insight from molecular analyses can be used to select appropriate morphological markers that define a robust classification, for example in the Bangiales Nägeli (Sutherland *et al.* 2011; Yang *et al.* 2020). However, in many cases taxa and classifications can be delimited only by molecular markers (Leliaert *et al.* 2014).

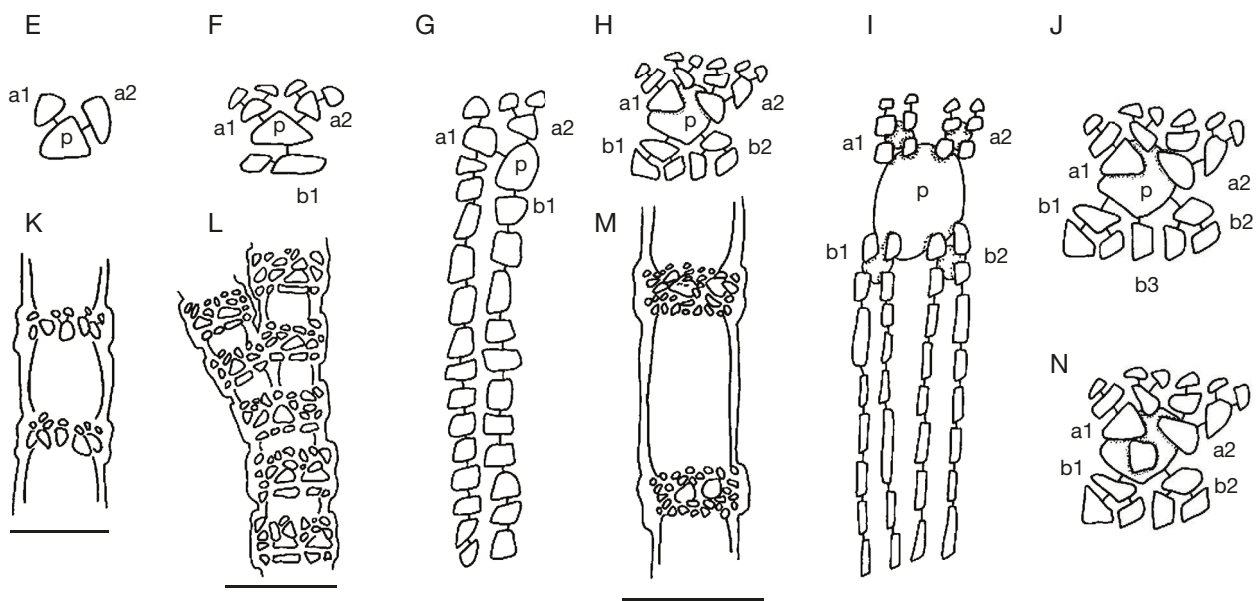
The red algal family Ceramiales Dumortier (order Ceramiales) is a good target for exploring molecular-guided issues because morphological similarities may not reflect true phylogenetic relationships in the family (Moe & Silva 1980). The Ceramiales is a large and complex family even after the sequential segregation of the Callithamniaceae Kützinger, and Wrangeliaceae J.Agardh (Choi *et al.* 2008; Díaz-Tapia *et al.* 2019; Guiry & Guiry 2022). In this paper, our goal is to reconstruct phylogenies in the Ceramiales C.Agardh ex Greville, the largest of 17 tribes of the Ceramiales, employing the approach advocated by Scotland *et al.* (2003) of using small numbers of selected morphological characters in concert with molecular data to reconstruct phylogenies. This provides many opportunities to examine morphological and molecular congruences/disparities and their consequences for taxonomy.

The Ceramiales is widely distributed in temperate and tropical waters; 11 filamentous marine genera (Table 1) include *c.* 270 recognized species (Guiry & Guiry 2022). They are constructed of uniaxial filaments with a characteristic vegetative anatomy ranging in size from a few millimetre up to 30 cm (Fig. 1). Most members of the Ceramiales can be readily assigned to the tribe by their characteristic vegetative anatomy: the central filament of axial cells is surrounded at the nodes (Fig. 1K-M), the junctions between axial cells, by rings of periaxial cells that give rise to cortical filaments (Fig. 1E-R). The currently recognized genera in the tribe are identified by gross morphological characters (e.g. compression of vegetative axes; radial versus planar branching) and anatomical features such as internal rhizoidal filaments cut-off from periaxial and cortical cells and the shape of cortical cells (Fig. 1E-N; Table 1; Norris 1993; Maggs & Hommersand 1993; Womersley 1998; Millar 2002; Cho *et al.* 2002, 2008a, b). The circumscription of genera and species has changed continually over the last decade (see Appendix 1), and our work here aims to resolve many of the current controversies.

In this study we have obtained molecular and morphological data for the last three decades (Maggs & Hommersand 1993; Maggs & Ward 1996; Barros-Barreto & Yoneshigue-Valentin 2001; Wattier *et al.* 2001; Maggs *et al.* 2002; Barros-Barreto *et al.* 2006; Wolf *et al.* 2011; Gomes *et al.* 2020). Global samples and DNA sequences include one or more representatives of all but one of the currently recognized non-parasitic genera. The plastid-encoded *rbcL* gene was selected as our primary molecular marker because a large dataset for the Ceramiales already existed, and *rbcL* analyses have shown good resolution at the species to tribal level (e.g. McIvor *et al.* 2001, 2002;



Number of cortical initials cells and descending filaments



Number of periaxial cells

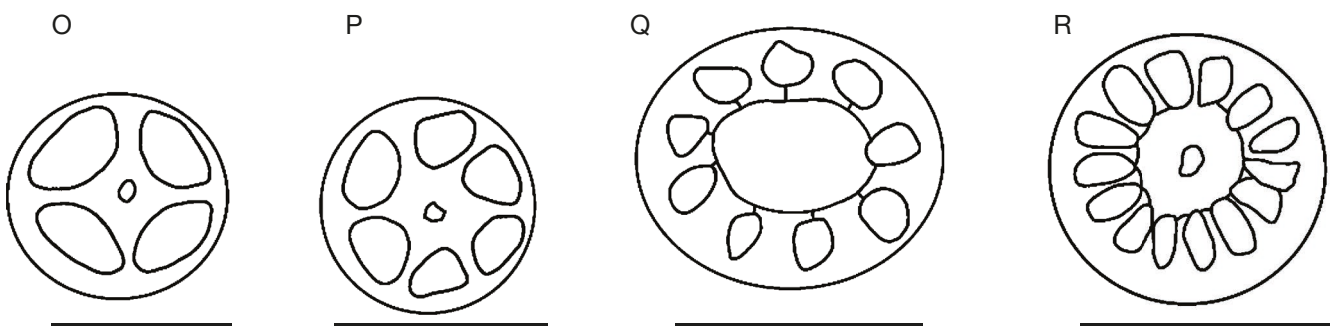


FIG. 1. — Diagnostic morphological features of the tribe Ceramieae: **A**, *Ceramium pallidum* (Kützling) Maggs & Hommersand; **B**, carposporophyte, *Pseudoceramium oliveirarum* Barros-Barreto, Maggs & M.A.Jaramillo, gen. nov., sp. nov.; **C**, tetrasporophyte, *Centroceras gasparrinii* (Meneghini) Kützling; **D**, male plant showing spermatangia, *Corallophila atlantica* (A.B.Joly & Ugadim) R.E.Norris; **E**, acropetal cells, *Yoneshigunea compta* (Børgesen) Barros-Barreto, Maggs & M.A.Jaramillo, comb. nov.; **F**, three cortical initial cells, *Gayliella dawsonii* (A.B.Joly) Barros-Barreto & F.P.Gomes; **G**, three cortical initial cells and two descending filaments, *Centroceras gasparrinii*; **H**, four cortical initial cells, *Stirkia fujiana* (Barros-Barreto & Maggs) Barros-Barreto & Maggs, comb. nov.; **I**, four cortical initial cells and descending filaments, *Corallophila atlantica*; **J**, five cortical initials including three descending filaments, *Ceramium secundatum* Lyngbye; **K**, *Yoneshigunea affinis* (Setchell & Gardner) Barros-Barreto, Maggs & M.A.Jaramillo, comb. nov. without descending filaments; **L**, one descending filament per periaxial cell, *Gayliella dawsonii* (A.B.Joly) Barros-Barreto & F.P.Gomes; **M**, two descending filaments, *Stirkia fujiana* (Barros-Barreto & Maggs) Barros-Barreto & Maggs, comb. nov.; **N**, five cortical initial cells, the fifth one over the periaxial cell, *Stirkia codicola* (J.Agardh) Barros-Barreto & Maggs, comb. nov.; **O**, transverse section showing four periaxial cells, *Yoneshigunea compta* (Børgesen) Barros-Barreto, Maggs & M.A.Jaramillo, comb. nov.; **P**, transverse section showing six periaxial cells, *Stirkia brasiliensis* (A.B.Joly) Barros-Barreto & Maggs, comb. nov.; **Q**, transverse section showing nine periaxial cells, Ceramieae sp. 5; **R**, transverse section showing 14 periaxial cells, *Centroceras gasparrinii*. Abbreviations: **a1**, first acropetal cell; **a2**, second acropetal cell; **b1**, first basipetal cell; **b2**, second basipetal cell; **b3**, third basipetal cell; **p**, periaxial cell. Scale bars: B, 500 µm; C, D, 200 µm; K, L, M, O-R, 100 µm.

Hommersand *et al.* 2006). For selected species we also generated smaller datasets for a mitochondrial marker (the 5' region of the mitochondrial gene cytochrome c oxidase I, COI-5P) and a nuclear marker (partial large subunit rRNA gene, LSU), and analysed each gene and a concatenated alignment. We show here how phylogenetic analyses of morphological features and DNA sequence data from nuclear and cytoplasmic markers can contribute to the identification of evolutionary trends and guide taxonomic decisions.

## MATERIAL AND METHODS

### SAMPLE COLLECTION AND CULTURE ISOLATES

Samples collected from a wide range of habitats in Europe and Brazil and from targeted localities and habitats around the world were processed in various ways (Appendix 2). All samples were examined alive and sorted into morphologically distinct groups, from which selected representative thalli were processed further. Brazilian samples were separated into morphologically different putative species and dried in silica gel. North Atlantic, Mediterranean, and Indo-Pacific smaller species were isolated into culture from spores or tips as described by Maggs & Ward (1996), and DNA was extracted from the cultured material as well as from fresh field-collected material. Samples of species >3 cm in size were dried directly in silica gel; smaller species from Japan and Brazil were preserved in 70% ethanol, and the material was sorted under a dissecting microscope. For morphological studies, the material was preserved in 4% seawater-Formalin, 70% ethanol, or rehydrated from silica gel-dried samples. Vouchers were prepared as microscope slide mounts or herbarium sheets and deposited in the Natural History Museum, London (BM), the Ulster Museum (BEL), the Instituto de Pesquisas do Jardim Botânico do Rio de Janeiro (RB) or the Museu Nacional – Universidade Federal do Rio de Janeiro (R).

### DNA EXTRACTION AND PCR AMPLIFICATION

DNA was extracted from 36 samples in addition to those for which sequences have previously been published (Appendix 2), by phenol/chloroform extraction (Maggs & Ward 1996) or using the Qiagen DNeasy Plant Mini Kit (Quiagen GmbH, Hilden, Germany) according to the manufacturer's instructions.

For PCR amplification of the *rbcL* locus, three pairs of primers were used (McIvor *et al.* 2002; Barros-Barreto *et al.* 2006). PCR was carried out in a final volume of 50 µL containing 2 µL of DNA, 2.5 mM MgCl<sub>2</sub> Taq Buffer 1X, 6.5 pmol of primer, 0.2 mM dNTP, and 1.6 to 2.5 U Taq DNA polymerase (Biotaq DNA polymerase, Boline, United Kingdom; or Taq DNA polymerase, Ludwig Biotec, Brazil). The amplifications were carried out using a Perkin Elmer DNA Thermal Cycler 480 (Perkin Elmer, Pangbourne, United Kingdom), a PTC-200 DNA Engine, or a PTC-100 TM programmable Thermal Cycler (MJ Research, Labtrade Inc., Miami, United States). The conditions followed McIvor *et al.* (2002) with an annealing temperature of 55°C. The fragments for sequencing reactions were purified either using PEG 20%, Microspine

(Millipore), or the High Pure PCR Product Purification Kit (Roche Diagnostics Ltd, Lewes, UK), according to the manufacturer's instructions. For COI-5P, primers and PCR conditions were as in Saunders (2005), and for the partial large subunit rRNA gene (LSU), primers and conditions followed Freshwater *et al.* (1999), with the addition of 5% DMSO in all reactions.

### DNA SEQUENCING

About 1250 base pairs (bp) of the *rbcL* gene were amplified, 680 bp of COI-5P and 920 bp of the LSU. The PCR-amplified products were directly sequenced using di-deoxy chain termination methodology, as previously described by Nam *et al.* (2000), using an ABI model 377 Genetic Analyzer with the ABI Prism BigDye Terminator Cycle Sequencing Ready Reaction Kit (Applied Biosystems, Sao Paulo, Brazil), or sequenced commercially (MGW Biotech, Martinsried, Germany; Fusion Antibodies, Belfast, Northern Ireland; and Macrogen, Korea). A combination of primers was used in the sequencing reactions (McIvor *et al.* 2002; Barros-Barreto *et al.* 2006).

### SEQUENCE ALIGNMENT AND PHYLOGENETIC ANALYSIS

Additional sequences were obtained from GenBank (March 2022). Distance (Neighbor-Joining, BioNJ; Gascuel 1997) analyses were conducted in Seaview 4.2.10 (Gouy *et al.* 2010) using 100 bootstrap replicates (Felsenstein 1985) in order to select diverging sequences; when identical, only sequences from different localities/studies were kept in our alignments. There was a total of 181 accessions (including outgroup) for the *rbcL* locus; 78 accessions for COI-5P; 72 for LSU rDNA; 71 for the concatenated alignment of the three markers (Appendix 2) and 122 for the reconstruction and integrative analyses (*rbcL* and morphology; Appendices 2; 3). Multiple alignments of DNA sequences were completed using Clustal X (Kroes *et al.* 2007) and Seaview 4.2.10 (Gouy *et al.* 2010). The concatenated alignment was assembled in Seaview 4.2.10. Because of missing data for some taxa, the *rbcL* alignment was trimmed to 1239 bp and the COI-5P alignment to 624 bp. For LSU, ambiguous sites were cut according to GBlocks (Castresana 2000) to 573 bp; the concatenated alignment was 2487 bp (*rbcL* = 1239 bp; LSU = 682 bp; COI-5P = 566 bp).

Sequence data were analysed by maximum likelihood (ML) using IQ-TREE (Nguyen *et al.* 2015; Trifinopoulos *et al.* 2016). Genes and codons were partitioned, and evolutionary models were selected by ModelFinder (Kalyaanamoorthy *et al.* 2017) using the Bayesian Information Criterion (BIC); partitioned models were used when appropriate (Chernomor *et al.* 2016); merge option was also included to increase model fit in IQ-TREE (Appendices 4; 5). Tree branches were tested by SH-like aLRT (Guindon *et al.* 2010) and bootstrapped with 1000 replicates.

Bayesian inference (BI) analyses were implemented using MrBayes 3.1.2 (Huelsenbeck & Ronquist 2001; Ronquist & Huelsenbeck 2003) or executed on the CIPRES Science Gateway (Miller *et al.* 2010). BI analyses consisted of two



TABLE 1. — All genera currently attributed to the tribe Ceramieae before this study (excluding two tiny parasitic genera: *Syringocolax* Reinsch and *Centrocercolax* A.B.Joly).

Genus and generitype	No. of species	Morphological and anatomical features currently used to delimit the genus
<i>Ardreanema</i> R.E.Norris & I.A.Abbott Type: <i>Ardreanema farifructa</i> R.E.Norris & I.A.Abbott	1	Terete; 3 periaxial cells; uniseriate gonimolobes
<i>Campylaephora</i> J.Agardh Type: <i>Campylaephora hypnaeoides</i> J.Agardh	5	Terete; 6-8 periaxial cells; cortication complete; internal rhizoidal filaments
<i>Carpoblepharis</i> Kützing nom. cons. Type: no designation	4	Compressed; 6-8 periaxial cells; cortication complete; tetrasporangia produced in stichidia-like structures
<i>Centroceras</i> Kützing Type: <i>Centroceras clavulatum</i> (C.Agardh) Montagne	11	Terete; 10-19 periaxial cells; 3 cortical initials per periaxial cell, cortication complete, basipetal only, in straight rows; spines at nodes; spermatangia on periaxial cells
<i>Ceramium</i> Roth Type: <i>Ceramium virgatum</i> Roth	195	Terete; 4-9 periaxial cells; 2, 4 or 5 cortical initials per periaxial cell, cortication basipetal and acropetal, complete or incomplete; internal rhizoids absent; spermatangia on cortical cells
<i>Corallophila</i> Weber van Bosse Type: <i>Corallophila kleiwegii</i> Weber-van Bosse	11	Terete; 6-8 periaxial cells; 4 cortical initials per periaxial cell, cortication complete, basipetal only, in straight rows; spermatangia on cortical cells
<i>Gayliella</i> T.O.Cho, L.J.McIvor & S.M.Boo Type: <i>Gayliella flaccida</i> (Harvey ex Kützing) T.O.Cho & L.J.McIvor	15	Terete; 4-8 periaxial cells; 3 cortical initials per periaxial cell, basipetal and acropetal, cortication incomplete, basipetal only, in straight rows; spines absent
<i>Herpochondria</i> F.Schmitz & Falkenberg Type: <i>Herpochondria corallinae</i> (G.Martens) Falkenberg	6	Compressed; 6-8 periaxial cells; cortication complete; lacking internal rhizoids, tetrasporangia produced in stichidia-like structures
<i>Microcladia</i> Greville Type: <i>Microcladia glandulosa</i> (Solander ex Turner) Greville	10	Branching planar, axes compressed; 6-8 periaxial cells; cortication complete; internal rhizoids absent in type species
<i>Reinboldiella</i> De Toni Type: <i>Reinboldiella schmitziana</i> (Reinbold) De Toni	6	Terete to compressed; 6 periaxial cells; cortication complete; tetrasporangia produced in stichidia-like structures

parallel runs, each of four Markov chains, and 30<sup>6</sup> generations were run (three times for each dataset) with sampling every 1000 generations. *RbcL* and COI-5P markers were partitioned (codon positions), the concatenated alignment was partitioned by gene and codon, and the model implemented independently for each gene/codon partition; all the parameters were unlinked. Burn-in fraction was set to 0.30%, and the generation numbers stopped when the Average Standard Deviation of split frequencies reached 0.015 (Appendices 4; 5).

The full taxon *rbcL* trees were rooted using five species as outgroups. For LSU analyses, two species of Ceramiaceae were used as outgroups. For COI-5P, the outgroups were members of the Callithamniaceae and Wrangeliaceae. *Antithamnion nipponicum* Yamada & Inagaki (Ceramiaceae, Antithamnieae Hommersand) was the outgroup for the concatenated alignment (Appendix 2).

#### MORPHOLOGICAL ANALYSIS

Eleven morphological characters were carefully selected from a set of 30 traits evaluated. Traits selected concern nodal development and tetrasporangia because they show phylogenetic signal (Barros-Barreto 2006). These characters were coded for all species based on examination of specimens and careful study of the literature (Fig. 1; Appendix 3). Morphological data are missing for some specimens for which sequences were obtained from GenBank; for these we included data

from literature when available. The alignment for the integrative analyses (*rbcL* + morphology) was assembled in Mesquite 3.6 (Maddison & Maddison 2019), and implemented using MrBayes 3.1.2 (Huelsenbeck & Ronquist 2001; Ronquist & Huelsenbeck 2003). For ML analyses implemented in IQ-TREE (Trifinopoulos *et al.* 2016) each dataset was performed separately for model selection (Appendices 4; 5) in ModelFinder (Kalyaanamoorthy *et al.* 2017); the analyses were combined and run following descriptions above. For the character state reconstruction, we used a reduced *rbcL* alignment analysed as explained above. Morphological characters were plotted on the terminals of the reduced *rbcL* tree using ggtree (Yu *et al.* 2017).

#### RESULTS

##### ANALYSES OF *RBCL* DATASET

The tribe Ceramieae is monophyletic with Bayesian support (Table 2). The genera *Centroceras* Kützing and *Gayliella* T.O.Cho, L.J.McIvor & S.M.Boo both constitute robust clades in the *rbcL*, integrative (*rbcL* + morphology) and concatenated analyses (Figs 2; 3; S1-S3). Within the Ceramieae, clades with strong support are named, and a new classification is proposed here (Figs 2; S1; S2; see Discussion). Clades are named by their constituent genera as follows: *Ceramium* Roth,

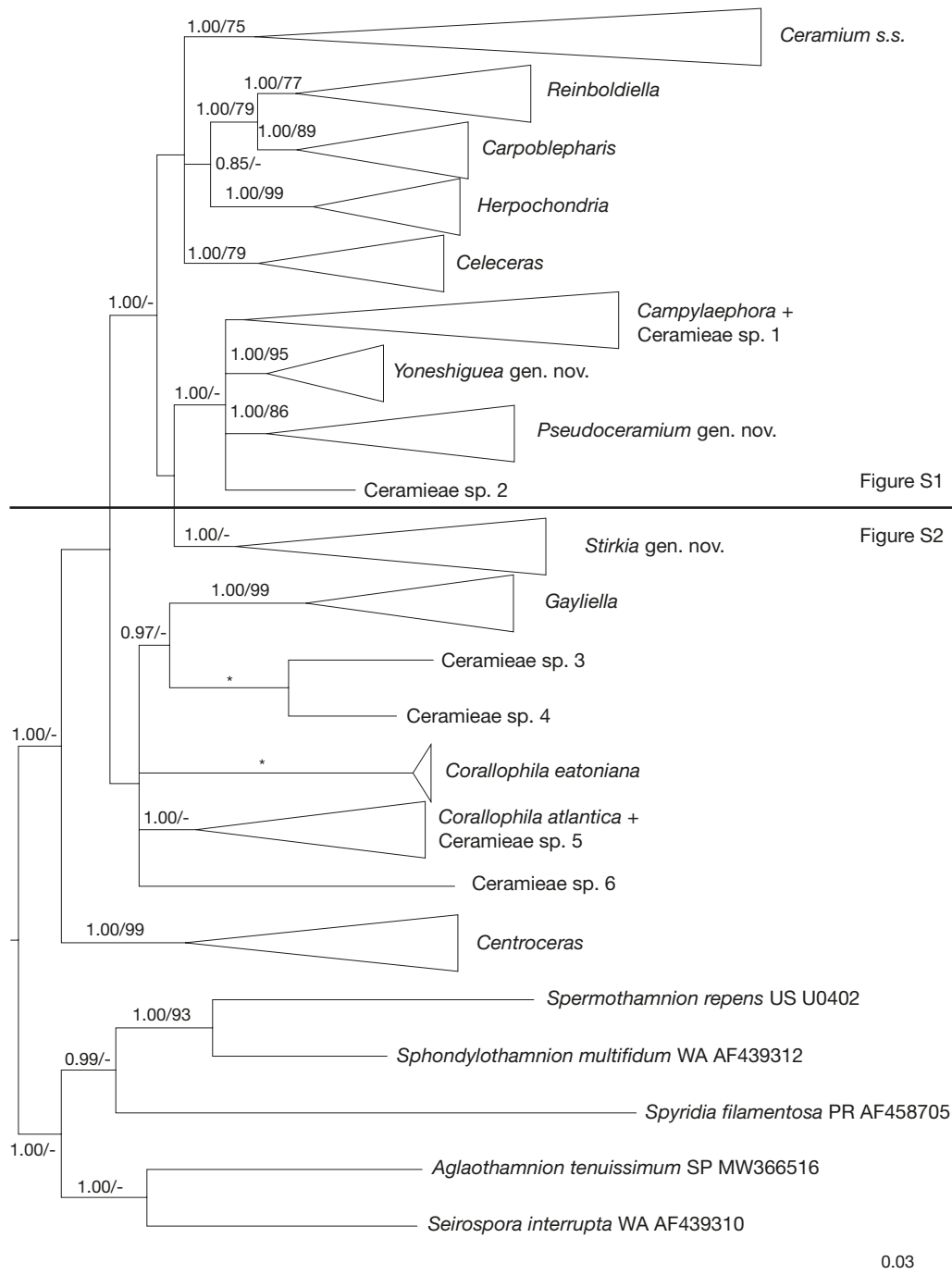


FIG. 2. — Phylogenetic reconstruction of the red algal tribe Ceramieae C.Agardh ex Greville inferred from *rbcL* gene sequences showing genera. The tree is the majority rule consensus tree resulting from Bayesian analysis. Values at the nodes represent posterior probability and bootstrap values for ML, support lower than 0.70 (PP) and 75 (BP) are not shown. Symbol: \*, full support.

*Reinboldiella* De Toni, *Carpoblepharis* Kützing, *Herpochondria* F.Schmitz & Falkenberg, *Celeceras* Kützing, *Campylaeophora* J.Agardh, *Pseudoceramium* Barros-Barreto & Maggs, gen. nov., *Yoneshiguea* Barros-Barreto, Maggs & M.A.Jaramillo, gen. nov., *Stirkia* Barros-Barreto & Maggs, gen. nov., *Gayliella*, *Corallophila* Weber-van Bosse and *Centroceras*. Relationships between clades were not supported (see Discussion).

#### ANALYSES OF COI-5P AND LSU DATASETS

The COI-5P phylogeny (Fig. S4) provides strong PP support for *Ceramium s.s.* and *Gayliella* as resolved in the *rbcL* analysis. Again, relationships among clades are not resolved. The LSU analysis (Fig. S5) resolves all the clades represented, including a robust *Gayliella*, but there is no resolution among clades.



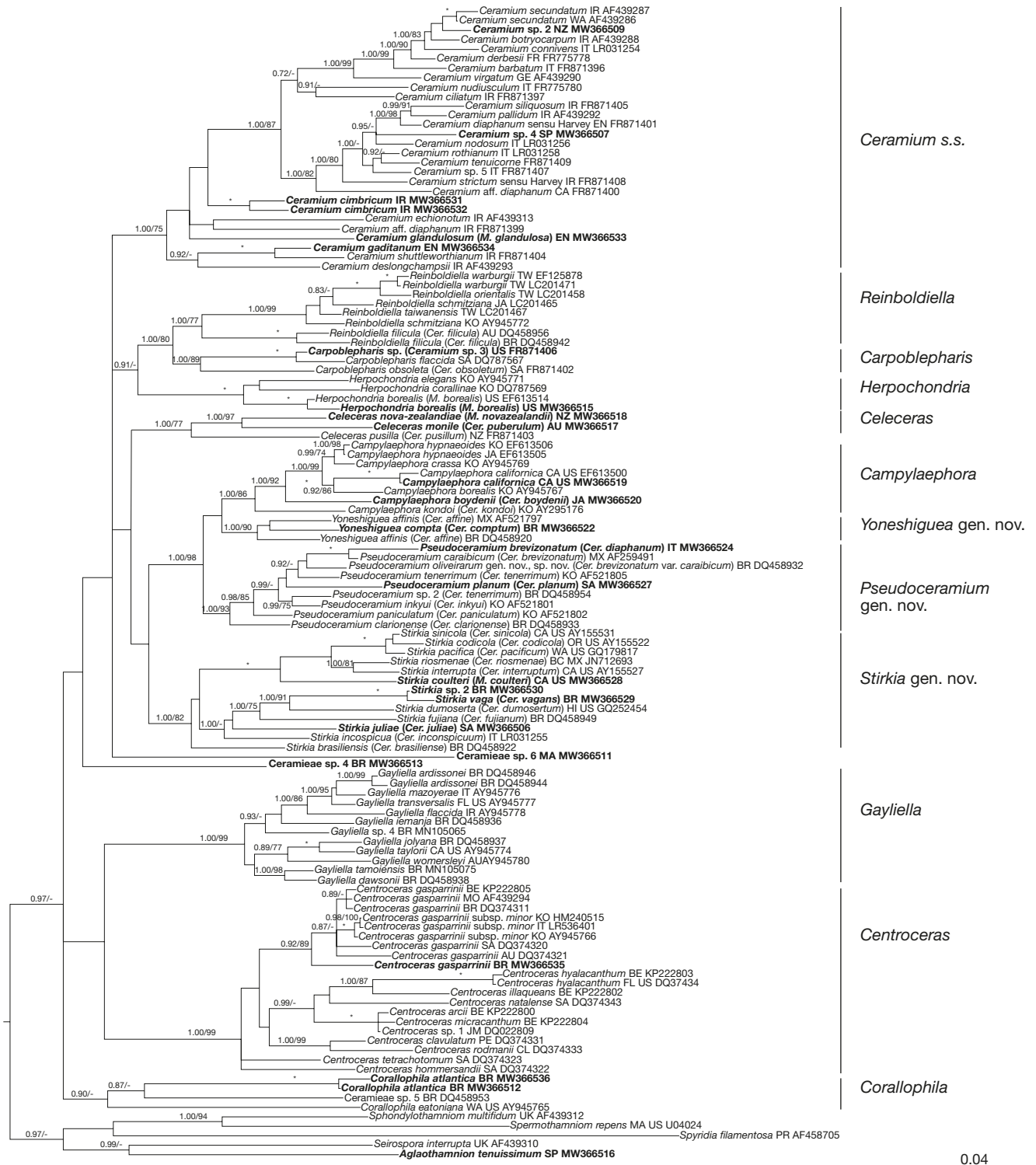


Fig. 3. — Phylogenetic reconstruction of the red algal tribe Ceramieae C.Agardh ex Greville inferred with an integrative approach based on *rbcl* gene and morphological characters. The tree is the majority rule consensus tree resulting from Bayesian analysis. Values at the nodes represent posterior probability and bootstrap values for ML; supports < 0.65 (PP) and 75 (BP) are not shown. Sequences generated in this study are in **bold**. Abbreviations: **AU**, Australia; **BE**, Bermuda; **BR**, Brazil; **NS CA**, Nova Scotia, Canada; **CL**, Chile; **DA**, Dutch Antilles; **DE**, Denmark; **EN**, England; **FR**, France; **FR PO**, French Polynesia; **GB TR**, British Overseas Territory of Tristan da Cunha; **GE**, Germany; **IR**, Ireland; **IT**, Italy; **JA**, Japan; **JM**, Jamaica; **KO**, South Korea; **MO**, Morocco; **MX**, Mexico; **BC MX**, Baja California, Mexico; **NA**, Namibia; **NO**, Norway; **NZ**, New Zealand; **PE**, Peru; **PR**, Puerto Rico; **SA**, South Africa; **SP**, Spain; **TW**, Taiwan; **AK US**, Alaska; **CA US**, California; **FL US**, Florida; **HI US**, Hawaii; **MA US**, Massachusetts; **OR US**, Oregon; **RI US**, Rhode Island; **WA US**, Washington; **WA**, Wales. Symbol: \*, full support.

TABLE 2. — Support values for genera. Abbreviations: **BP**, bootstrap (1000 replicates IQ-TREE); **PP**, posterior probability (Bayesian Inference); **ND**, no data. Symbol: —, no support.

Markers Genera	<i>rbcl</i>		Concatenated ( <i>rbcl</i> + LSU + COI)		Integrative ( <i>rbcl</i> + morphology)		Partial LSU rRNA		COI-5P	
	PP	BP	PP	BP	PP	BP	PP	BP	PP	BP
<i>Ceramium</i>	1.00	75	1.00	98	1.00	75	1.00	100	0.97	61
<i>Reinboldiella</i>	1.00	77	ND	ND	1.00	77	ND	ND	ND	ND
<i>Carpoblepharis</i>	1.00	89	ND	ND	1.00	89	ND	ND	ND	ND
<i>Herpochondria</i>	1.00	99	ND	ND	1.00	100	1.00	99	ND	ND
<i>Celeceras</i>	1.00	79	ND	ND	1.00	77	ND	ND	ND	ND
<i>Campylaephora</i>	0.69	—	0.86	—	1.00	86	—	—	0.99	—
<i>Yoneshigaea</i> gen. nov.	1.00	95	1.00	100	1.00	90	ND	ND	ND	ND
<i>Pseudoceramium</i> gen. nov.	1.00	86	1.00	98	1.00	93	ND	100	ND	ND
<i>Stirkia</i> gen. nov.	1.00	57	—	—	1.00	82	—	—	—	25
<i>Gayliella</i>	1.00	99	1.00	92	1.00	99	1.00	97	—	—
<i>Corallophila</i>	—	—	1.00	83	0.90	21	—	—	—	—
<i>C. atlantica</i> + Ceramieae sp. 5	1.00	42	0.94	73	0.87	46	ND	ND	0.99	—
<i>Centroceras</i>	1.00	99	1.00	99	1.00	99	1.00	99	—	—
							(partial)	(partial)		
Ceramieae	1.00	34	—	—	0.97	—	—	—	1.00	35

ANALYSES OF CONCATENATED DATASET AND INTEGRATIVE EVIDENCE

The topologies obtained using ML and BI were similar, and the clades, with a reduced taxon set, are like those obtained with the full taxon *rbcl* dataset (Figs 2; S1; S2). The topology of the combined evidence (*rbcl* + morphology) analysis is congruent with the *rbcl* reconstruction. Support values are similar for all branches, and much higher for the genus *Campylaephora* (BI = 1.00/BS = 86), when morphological data are included (Fig. 3; Table 2).

MORPHOLOGICAL ANALYSIS

The phylogenetic distributions of currently used diagnostic characters for genera are displayed (Fig. 4). Morphological characters, vegetative and reproductive, varied among and within clades, although several had previously been considered diagnostic of particular genera. Species with compressed thalli were scattered among species with terete thalli in more than half of the genera, although the genera *Corallophila*, *Gayliella*, *Pseudoceramium* Barros-Barreto & Maggs, gen. nov., *Yoneshigaea* Barros-Barreto, Maggs & M.A.Jaramillo, gen. nov. and *Centroceras* had terete thalli only. Internal rhizoidal filaments were present in the genus *Campylaephora* and in *Herpochondria borealis* Barros-Barreto & Maggs, comb. nov. (synonym: *Microcladia borealis* Ruprecht), *Pseudoceramium planum* Barros-Barreto & Maggs, comb. nov. (synonym: *Ceramium planum* Kützing), and Ceramieae sp. 5 (synonym: *Ceramium nitens* (C.Agardh) J.Agardh). The level of cortication was homoplastic, varying in almost all clades from partial to complete, being fixed only in *Gayliella* (partial), *Centroceras* and *Corallophila* (complete). The number of cortical initials per periaxial cell varied in all clades except *Corallophila* and *Herpochondria*, which have four initials, and *Centroceras* and *Gayliella*, with three initials. The degree of covering of tetrasporangia (naked; partially covered by filaments; immersed) was highly homoplastic, varying within each clade. The position of tetrasporangia on the nodes also varied in the tree and within each clade.

DISCUSSION

PHYLOGENY AND TAXONOMIC REVISION OF CERAMIEAE

The tribe Ceramieae (Ceramieaceae) is reconstructed here to include twelve genera with varying levels of support (Table 4). Most clades within the tribe are strongly supported in the BI tree and moderately supported by BP values (Table 2); relationships among clades are not well resolved. Taxonomic implications of our conclusions are discussed here with nomenclatural proposals at the end of the article.

The clade *Ceramium* includes the generic type species *C. virgatum* Roth. In this revised circumscription, *Ceramium sensu stricto* is a North Atlantic genus, with Mediterranean representatives, that has been introduced to New Zealand and probably elsewhere (Bruce & Saunders 2015). None of the numerous schemes used to subdivide the genus based on the degree of cortication or the position of tetrasporangia (e.g. Agardh 1851; Nakamura 1965; Table 3) has any validity (Fig. 4). Our revised circumscription of a monophyletic *Ceramium* results in a large number of nomenclatural changes because members of most of our other clades include species currently attributed to *Ceramium*.

The *Ceramium* clade includes the type species of *Microcladia* Greville which was segregated from *Ceramium* by its compressed thalli, alternate, distichous branching, and continuous cortication of small angular cells (Hommsand 1963; Maggs & Hommsand 1993). The type species, *M. glandulosa* Solander ex Turner (now *Ceramium glandulosum* (Solander ex Turner) Barros-Barreto & Maggs, comb. nov.) is included in *Ceramium sensu stricto*. Our analyses show that the characters that unite *Microcladia* species have all arisen more than once within the Ceramieae (Fig. 4). The type species of *Microcladia* is in the same clade as the type species of the older genus, *Ceramium*, and *Microcladia* is regarded here as a synonym of *Ceramium*. Further molecular analyses of the other five recognized species of *Microcladia*, placed in various clades within the phylogeny, are necessary to assign them to the appropriate clade. Nomenclatural changes are enumerated below.

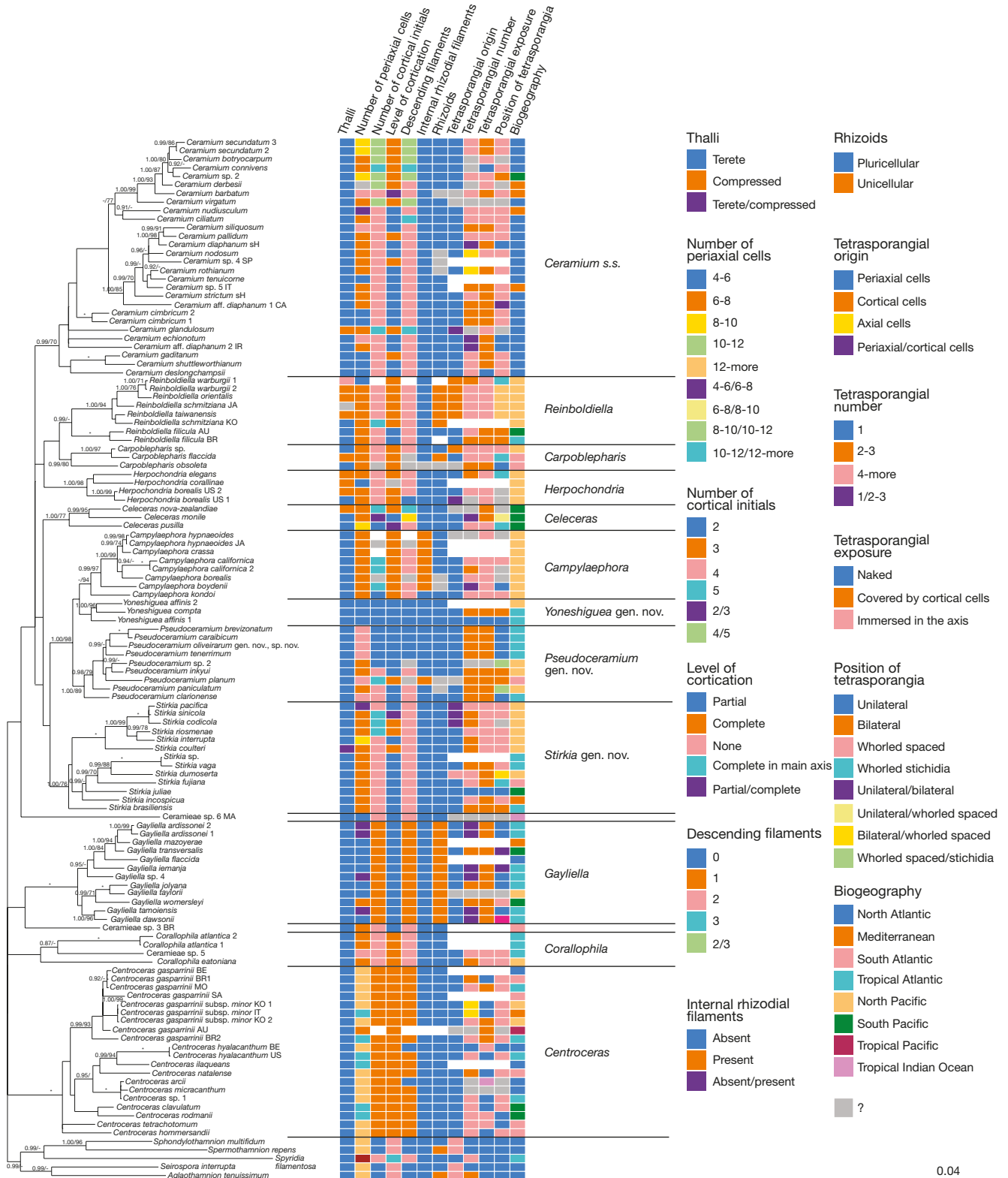


Fig. 4. — Reconstruction of character evolution by mapping morphological characters onto the Bayesian tree inferred on *rbcL* gene. Geographical distribution is given for all the samples. Values at the nodes represent posterior probability, values <0.8 are not shown. Abbreviations: See Figure 3.

In the *Reinboldiella* + *Carpoblepharis* + *Herpochondria* clade, *Reinboldiella* and *Carpoblepharis* are closely related. Okamura (1901, 1903) considered *Reinboldiella* a synonym of *Carpobleph-*

*aris* but others have viewed the two genera as distinct because of the former's small size and prostrate habit (Feldmann & Mazoyer 1937; Hommersand 1963; Lin & Hommersand



TABLE 3. — Generic synonyms of *Ceramium* Roth.

Name	Authority	References
<i>Episperma</i>	Rafinesque (1814)	Schneider & Wynne 2007
<i>Dictiderma</i>	Bonnemaison (1822: 185)	Agardh 1852; Silva 1952
<i>Boryna</i>	Grateloup in Bory (1822: 412)	Agardh 1852; De Toni 1903
<i>Gaillonia</i>	Rudolphi (1831)	Schneider & Wynne 2007
<i>Hormoceras</i>	Kützing (1841: 730)	Agardh 1852; De Toni 1903
<i>Gongroceras</i>	Kützing (1841: 730)	Agardh 1852; De Toni 1903
<i>Echinoceras</i>	Kützing (1841: 731)	Agardh 1852; De Toni 1903
<i>Acanthoceras</i>	Kützing (1841: 731)	Agardh 1852; De Toni 1903
<i>Chaetoceras</i>	Kützing (1847: 34)	Agardh 1852; De Toni 1903
<i>Trichoceras</i>	Kützing (1849: 680)	Agardh 1852; De Toni 1903
<i>Celeceras</i>	Kützing (1849: 683)	Agardh 1852; De Toni 1903
<i>Pteroceras</i>	Kützing (1849: 690)	Agardh 1852; De Toni 1903
<i>Herpoceras</i>	Cramer (1864: 76, 104)	Hommersand 1963; Womersley 1978
<i>Ceramothamnion</i>	Richards (1901: 264)	Mazoyer 1938; Hommersand 1963
<i>Ceramiella</i> (now recognized as a synonym of <i>Corallophila</i> )	Børgesen (1953: 47)	Hommersand 1963

2007). Here the genera form independent, well-supported clades and are recognized as distinct. *Ceramium filiculum* Harvey ex Womersley is here transferred to *Reinboldiella filicula* (Harvey ex Womersley) Barros-Barreto & Maggs, comb. nov. Besides the phylogenetic position, they share the following morphological characters: six periaxial cells, four cortical initials, and unicellular rhizoids (also seen in *Gayliella*, a very well-established genus within the Ceramieae). *Ceramium obsoletum* C.Agardh is here transferred to *Carpoblepharis obsoleta* (C.Agardh) Barros-Barreto & Maggs, comb. nov. based on its phylogenetic position and the presence of stichidial tetrasporangia (Hommersand 1963; Wynne 1985a).

*Herpochondria* species form a well-supported clade sister to *Carpoblepharis* and *Reinboldiella* (with moderate support BI = 0.85; Figs 2; S1), including the type species *H. corallinae* (G.Martens) Falkenberg and *H. elegans* (Okamura) Itono from the western Pacific and two accessions of *Microcladia borealis* Ruprecht (now *Herpochondria borealis* (Ruprecht) Barros-Barreto & Maggs, comb. nov.) from the eastern Pacific. All of them have compressed axes (Fig. 4). One of the characteristic features of *Herpochondria* is the formation of tetrasporangia in stichidia-like structures, although in *H. borealis* the tetrasporangia are bilateral rather than whorled. Wynne (1985b) noted that species assigned to both *Herpochondria* and *Microcladia* had eight periaxial cells of unequal size and continuous cortication.

The next strongly supported clade in the *rbcL* analysis (Figs 2; S1) comprises three species. Here we reinstate the genus *Celeceras*, with the generic type *Celeceras monile* (Hooker & Harvey) Kützing (synonym: *Ceramium puberulum* Sonder), based on a specimen from Australia which was investigated in a monograph on this group (Womersley 1978). All species in the clade have multicellular rhizoids, lack internal rhizoidal filaments, and tetrasporangia are formed from periaxial cells (Fig. 4).

*Campylaephora* is resolved in *rbcL* analyses (Figs 2; 3; S1; S3). This genus was erected for its internal rhizoids and hook-shaped tips to the branches (Agardh 1851); the formation of secondary pit connections by these rhizoidal filaments is also

considered significant (Cho *et al.* 2008b). The phylogenetic relationships suggest the inclusion in *Campylaephora* of *C. boydenii* (E.S.Gepp) Barros-Barreto & Maggs, comb. nov. (synonym: *Ceramium boydenii* E.S.Gepp) and *C. kondoi* (Yendo) Barros-Barreto & Maggs, comb. nov. (synonym: *Ceramium kondoi* Yendo) which have internal rhizoids but lack secondary pit connections.

*Yoneshigaea* Barros-Barreto, Maggs & M.A.Jaramillo, gen. nov. is proposed for two species forming only acropetal (no basipetal) cortical initials from the periaxial cell (Figs 1E, K; 4), typified by *Yoneshigaea affinis* (Setchell & N.L.Gardner) Barros-Barreto, Maggs & M.A.Jaramillo, comb. nov. (synonym: *Ceramium affine* Setchell & N.L.Gardner).

The next lineages include species currently recognized as *Ceramium*. One of them contains species from the Tropical Atlantic as well as the Northwestern Pacific. All Brazilian representatives have pseudoperiaxial cells cut off laterally from periaxial cells (Barros-Barreto *et al.* 2006). We did not have access to NW Pacific samples to check this characteristic. A new genus *Pseudoceramium* Barros-Barreto & Maggs, gen. nov. is proposed here, typified by *Pseudoceramium oliveirarum* Barros-Barreto, Maggs & M.A.Jaramillo, gen. nov., sp. nov. (synonym: *Ceramium brevizonatum* var. *caraibicum* H.E.Petersen & Børgesen from Brazil). This genus includes seven species.

The next, morphologically diverse, clade has strong Bayesian support (Figs 2; 3; S2). The new genus *Stirkia* Barros-Barreto & Maggs, gen. nov. typified by *Stirkia fujiana* (Barros-Barreto & Maggs) Barros-Barreto & Maggs, comb. nov. (synonym: *Ceramium fujianum* Barros-Barreto & Maggs) from Brazil, is proposed here for this clade. It includes *S. juliae* (A.Millar) Barros-Barreto & Maggs, comb. nov. (synonym: *Ceramium juliae* A.Millar) and species with tetrasporangial stichidia such as *S. fujiana* (Barros-Barreto & Maggs) Barros-Barreto & Maggs, comb. nov. The new genus *Stirkia* Barros-Barreto & Maggs, gen. nov. is supported by molecular data presenting a molecular signature (a shared distinct sequence of nucleotides) in the *rbcL* alignment. This molecular approach to generic circumscription has been used in fungi (Redecker

TABLE 4. — All genera currently attributed to the tribe Ceramieae after this study (in addition to two tiny parasitic genera: *Syringocolax* Reinsch and *Centrocerocolax* A.B.Joly).

Genus and generic type	No. of species	Morphological and anatomical features currently used to delimit the genus
<i>Ardreanema</i> R.E.Norris & I.A.Abbott Type: <i>Ardreanema farifructa</i> R.E.Norris & I.A.Abbott	1	Terete; 3 periaxial cells; uniseriate gonimolobes
<i>Campylaephora</i> J.Agardh Type: <i>Campylaephora hypnaeoides</i> J.Agardh	12	Terete; 6-8 periaxial cells; cortication complete; internal rhizoidal filaments; tetrasporangia immersed in the axis
<i>Carpoblepharis</i> Kützing nom. cons. Type: no designation	4	Terete to compressed; 6-8 periaxial cells; cortication complete; tetrasporangia produced unilaterally, whorled or in stichidia-like structures
<i>Celeceras</i> Kützing Type: <i>Celeceras monile</i> (Hook. & Harv.) Kützing	3	Terete to compressed; 6-10 periaxial cells; cortication partial to complete; internal rhizoidal filaments, tetrasporangia naked to covered by cortical cells
<i>Centroceras</i> Kützing Type: <i>Centroceras clavulatum</i> (C.Agardh) Montagne	16	Terete; 10-19 periaxial cells; 3 cortical initials per periaxial cell, cortication complete, basipetal only, in straight rows; spines at nodes; spermatangia on periaxial cells
<i>Ceramium</i> Roth Type: <i>Ceramium virgatum</i> Roth	29	Terete; 4-9 periaxial cells; 4 or 5 cortical initials per periaxial cell, cortication basipetal and acropetal, complete or incomplete; spermatangia on cortical cells
<i>Corallophila</i> Weber van Bosse Type: <i>Corallophila kleiwegii</i> Weber van Bosse	2	Terete; 6-8 periaxial cells; 4 cortical initials per periaxial cell, cortication complete, basipetal only, in straight rows; spermatangia on cortical cells
<i>Gayliella</i> T.O.Cho, L.J.McIvor & S.M.Boo Type: <i>Gayliella flaccida</i> (Harvey ex Kützing) T.O.Cho & L.J.McIvor	16	Terete; 4-8 periaxial cells; 3 cortical initials per periaxial cell, basipetal and acropetal, cortication incomplete, only one basipetal cell, in straight rows
<i>Herpochondria</i> F.Schmitz & Falkenberg Type: <i>Herpochondria corallinae</i> (G.Martens) Falkenberg	6	Compressed; 6-8 periaxial cells; cortication complete; lacking internal rhizoids, tetrasporangia produced in stichidia-like structures
<i>Pseudoceramium</i> Barros-Barreto & Maggs, gen. nov. Type: <i>Pseudoceramium oliveirarum</i> Barros-Barreto, Maggs & M.A.Jaramillo, gen. nov., sp. nov.	8	TereteBranching planar, axes compressed; 7-10 periaxial cells, pseudoperiaxial cells present in some species; cortication mainly incomplete; 2-3 tetrasporangia covered by cortical cells
<i>Reinboldiella</i> De Toni Type: <i>Reinboldiella schmitziana</i> (Reinbold) De Toni	5	Terete to compressed; 6-8 periaxial cells; cortication partial to complete; tetrasporangia produced bilaterally, whorled or in stichidia-like structures
<i>Stirkia</i> Barros-Barreto & Maggs, gen. nov. Type: <i>Stirkia fujiana</i> (Barros-Barreto & Maggs) Barros-Barreto & Maggs, comb. nov.	17	Terete or terete to compressed; 6-10 periaxial cells; 4-5 cortical initials; partial to complete cortication
<i>Yoneshiguela</i> Barros-Barreto, Maggs & M.A.Jaramillo, gen. nov. Type: <i>Yoneshiguela affinis</i> (Setchell & Gardner) Barros-Barreto, Maggs & M.A.Jaramillo, comb. nov.	3	Terete; 4-6 periaxial cells; 2 cortical initials, acropetal only; 1-3 tetrasporangia, naked to covered by cortical cells

*et al.* 2007), some red algae (e.g. *Pibiella liagoraciphila* Huisman, Sherwood & Abbott), and some plants (Kadereit *et al.* 2012). It is common to use DNA-based characters for taxon circumscription (Aime *et al.* 2021; Sciuto *et al.* 2021)

*Gayliella* is strongly supported in all analyses (Figs 2; 3; S2-S4) and it is well-circumscribed (Cho *et al.* 2008a; Gomes *et al.* 2020; Huaqiang *et al.* 2020). The character combination of unicellular rhizoids and three cortical initials is unique to *Gayliella*. Neither of these two traits is unique, as unicellular rhizoids are also found in *Reinboldiella*, and periaxial cells each producing two acropetal and one basipetal corticating filament is also seen in *Centroceras* (Fig. 1F, G, L). This clade is composed of 11 of the 15 known *Gayliella* species (sequences for four species are presently unavailable).

*Corallophila* is a well-supported clade in the concatenated analysis (Table 2; Fig. S3), and it is in all analyses despite its low support. *Corallophila* includes *C. atlantica* (A.B.Joly &

Ugadam) R.E.Norris and Ceramieae sp. 5 (synonym: *Ceramium nitens* (C.Agardh) J.Agardh), both from Brazil (Figs 2; S2). *Corallophila* species differ from *Centroceras* and *Ceramium* in some morphological characters (they always lack involuclal branches surrounding the gonimolobes whereas *Centroceras* and *Ceramium* normally form them; Norris 1993). It is likely that *Corallophila* is recognizable only by a combination of characters, including the development of cortication (Norris 1993; Cho *et al.* 2000: fig. 1I). In the LSU and COI-5P analyses, *Corallophila huysmansii* (Weber Bosse) R.E.Norris from Hawaii did not group with other *Corallophila* species in this study (Figs S4; S5). This genus requires further study to confirm its status.

*Centroceras* is a very well-circumscribed and strongly supported clade. Our analyses include three samples of *Centroceras clavulatum* (C.Agardh) Montagne, one from Peru, the type locality (Figs S2-S4). *Centroceras clavulatum* has been shown to consist

of at least eight species rather than a single cosmopolitan one (Won *et al.* 2009; Won 2010; Schneider *et al.* 2015). Furthermore, *Centroceras gasparrinii* subsp. *minor* M.A. Wolf, A. Buosi, A.S. Juhmani & A. Sfriso described recently from Korea and the Mediterranean, was distinguished based on molecular sequence data and having one less periaxial cell than *C. gasparrinii* (Meneghini) Kützing (12, and 13-19, respectively) (Wolf *et al.* 2019).

#### CHARACTER EVOLUTION WITHIN CERAMIEAE

All morphological characters evaluated are homoplastic, thus, none can be used in isolation as diagnostic for genera within the Ceramieae. Compressed axes were considered diagnostic for *Microcladia*, but they have evolved independently in several clades in the Ceramieae (Fig. 4). Likewise, the degree of cortication is in general a highly plastic characteristic in the tribe. *Ceramium* s.s. contains species that range in cortication from restricted to the nodes to completely covering the internodal axes (Fig. 4; Maggs *et al.* 2002; Skage *et al.* 2005), confirming that degree of cortication cannot be used to segregate genera. Despite this, there may be an evolutionary trend towards complete cortication in *Ceramium* s.s. In the North Atlantic clade, each lineage (Figs 4; S1) has species with incomplete cortication, e.g. *C. circinatum* (Kützing) J. Agardh and *C. strictum* Roth, sister to those that can form a complete cortex, e.g. *C. pallidum* (Kützing) Maggs & Hommersand, and *C. secundatum* Lyngbye.

Detailed anatomy of the cortex is diagnostic at the clade level. Parallel rows of isodiametric cortical cells are found in *Centroceras* and *Corallophila*. The number of cortical initials developing from each periaxial cell is diagnostic at the clade level in most cases, separating *Centroceras* (three initials) from *Corallophila* (four initials; Norris 1993; Cho *et al.* 2000; Won *et al.* 2009; Schneider *et al.* 2015). There has been a character state change in one lineage of *Ceramium* s.s., from four cortical initials (two ascending and two descending filaments) to five cortical initials (two ascending and two or three descending filaments) in *Ceramium pallidum* and closely related species (Maggs *et al.* 2002). Members of *Yoneshigaea* Barros-Barreto, Maggs & M.A. Jaramillo, gen. nov. such as *Y. compta* (Børgesen) Barros-Barreto, Maggs & M.A. Jaramillo, comb. nov. and *Y. affinis* (Setchell & N.L. Gardner) Barros-Barreto, Maggs & M.A. Jaramillo, comb. nov. never cut off any basipetal cortical initials. *Centroceras* and *Gayliella* both have only one basipetal cell (Fig. 4; Cho *et al.* 2008a).

Rhizoids and the nature of attachment organs are taxonomically important in other ceramialean groups (Maggs & Hommersand 1993; Zuccarello & West 2006; Bustamante *et al.* 2017, 2019; Díaz-Tapia *et al.* 2017). Unicellular rhizoids are synapomorphic for *Gayliella* and *Reinboldiella* (except *R. filicula* (Harvey ex Womersley) Barros-Barreto & Maggs, comb. nov.) and Ceramieae sp. 4.

Few reproductive characters are meaningful at higher taxonomic levels in the Ceramieae, as they are relatively uniform. However, some male reproductive characters are of evolutionary significance in the Callithamnieae (McIvor *et al.* 2002), and the origin of the spermatangia from the pericentral cells in *Centroceras* rather than from the cortical cells is a unique synapomorphy for the genus (Hommersand 1963; Norris 1993).

Our analyses show that position and exposure of tetrasporangia are meaningful characters within some clades, although particular character states are found in several clades, e.g. tetrasporangia are immersed in the thalli in some species of *Stirikia* Barros-Barreto & Maggs, gen. nov. and unilateral in *Gayliella* and *Pseudoceramium* Barros-Barreto & Maggs, gen. nov. (Fig. 4). Stichidia-like tetrasporangial branchlets are seen in diverse clades, e.g. *Herpochondria*, *Reinboldiella*, *Carpoblepharis*, and *Stirikia* Barros-Barreto & Maggs, gen. nov. It is clear, for this tribe, that individual morphological characters cannot delineate natural groups. Samples showing similar morphology may be phylogenetically distant, for example, *Reinboldiella filicula* (Harvey ex Womersley) Barros-Barreto & Maggs, comb. nov. (Fig. 3), which resembles *Stirikia brasiliensis* (A.B. Joly) Barros-Barreto & Maggs, comb. nov. (Fig. 4; see Barros-Barreto *et al.* 2006) showed 9% and 23% genetic divergence in *rbcL* and COI-5P, respectively. Combinations of characters can nevertheless define clades and genera, such as *Gayliella* (Gomes *et al.* 2020).

In summary, the tribe Ceramieae shows a high degree of morphological homoplasy as well as extreme phenotypic plasticity. The genus *Ceramium* is non-monophyletic (Seo *et al.* 2003; Barros-Barreto *et al.* 2006; Cho *et al.* 2008a, b). In this work we propose several genera based on our phylogenetic analyses. Although support is not very strong (for some clades) we considered better to make proposals that can be further tested by adding more data such as phylogenomic approaches (Díaz-Tapia *et al.* 2019) rather than to retain a *Ceramium* concept that is non-monophyletic. We believe that molecular phylogenies inferred from a geographically representative sampling are crucial to the classification of Ceramieae. Molecular data are required to understand generic circumscriptions and evolutionary relationships, and based on the data generated in the present study we proposed the following taxonomic revision.

#### NOMENCLATORIAL PROPOSALS

Family CERAMIACEAE Dumortier  
Tribe CERAMIEAE C. Agardh ex Greville  
Genus *Campylaephora* J. Agardh

*Campylaephora boydenii* (Gepp)  
Barros-Barreto & Maggs, comb. nov.

*Ceramium boydenii* E.S. Gepp, *Journal of Botany, London* 42: 164, pl. 460, figs 1-3 (Gepp 1904).

HOLOTYPE. — **China**. Wei-hei-wai, Liu-kung-tao Island. Illustration in Gepp (1904).

EPITYPE. — **Japan**. Sea of Japan, Fukui Prefecture, Echizen, Kuriya, Drift, 5.VII.1971, *Hommersand s.n.* (epi-, here designated, NCU [NCU-A-0004403]).

#### NOTES

In the publication E. S. Gepp did not designate a holotype, but he included (and referred to in the description) an illustration that we designate as the holotype. However, the figures are not very detailed and are not useful for identification. We



therefore designate a collection made in Japan by M. Hommersand (specimen NCU-A-0004403) as an epitype. The latter is a very complete specimen, with reproductive structures present, and was the source of tissue for obtaining the DNA sequence data in this study.

*Campylaephora gardneri* (Kylin)  
Barros-Barreto & Maggs, comb. nov.

*Ceramium gardneri* Kylin, *Lunds Universitets Årsskrift, Ny Följd, Andra Afdelningen* 37 (2): 29 (Kylin 1941).

LECTOTYPE. — **United States**. California, Monterey County, Pescadero Point (Kylin 1941: 29), 36°33'43.7328"N, 121°57'11.2932"W, on rocks and algae in the lower littoral, V.1916, 2248 *N. L. Gardner* (lecto-, designated by Cho *et al.* [2002: 558], UC[UC2076252]).

NOTE

Cho *et al.* (2002: 558) noted that there are two tetrasporangial specimens attached on the herbarium sheet of the published exsiccata *Phycotheca Boreali-Americana* (P. B.-A.) XLV, no. 2248, at LD. Cho designated both of these thalli as the lectotype. Isotypes are in UC and NY, and thus published exsiccata (P. B.-A.) in other herbaria holding would also be isotypes.

*Campylaephora kondoi* (Yendo)  
Barros-Barreto & Maggs, comb. nov.

*Ceramium kondoi* Yendo, *Botanical Magazine, Tokyo* 34: 9 (Yendo 1920).

SYNTYPE LOCALITY. — “Hab. in mari Japonia, ad insulam Rishiri, in portu Otaru (Kingo Kondo), portu Hakodate (ipse), prov. Echigo (Nou Fisheries School, no. 12)” (Yendo 1920: 9).

LECTOTYPE. — **Japan**. Hokkaido, Harius (lecto-, designated by Cho *et al.* [2002: 564], SAP[SAP 67]).

NOTES

Cho *et al.* (2002: 564) gave “Harius, Hokkaido, Japan” as the type locality.

*Campylaephora sungminbooi* (J.R.Hughey & G.H.Boo)  
Barros-Barreto & Maggs, comb. nov.

*Ceramium sungminbooi* J.R.Hughey & G.H.Boo, *Botanica Marina* 59 (4): 215, figs 1-5 (21-16) (Hughey & Boo 2016).

TYPE LOCALITY. — **South Korea**. Jindo, Hoedong, 34°25'20.6"N, 126°20'50.5"E (Hughey & Boo 2016: 215).

HOLOTYPE (TETRASPOROPHYTE). — **South Korea**. Jindo, Hoedong, 34°25'20.6"N, 126°20'50.5"E, attached to pebbles on the mudflat, 28.II.2002, *S.M. Boo, G.Y. Cho & E.C. Yang s.n.* (holo-, CNUK[CNU065811]).

ISOTYPES. — **South Korea**. Jindo, Hoedong, 34°25'20.6"N, 126°20'50.5"E, 28.II.2002 (iso-, CNUK[CNU065809, CNU065810]).

Genus *Carpoblepharis* Kützing

*Carpoblepharis obsoleta* (C.Agardh)  
Barros-Barreto & Maggs, comb. nov.

*Ceramium obsoletum* C.Agardh, *Species algarum rite cognitae, cum synonymis, differentiis specificis et descriptionibus succinctis. Voluminis secundi, Sectio prior*: 145 (Agardh 1828).

TYPE LOCALITY. — **South Africa**. Cape of Good Hope (Silva *et al.* 1996: 400).

LECTOTYPE. — **South Africa**. Cape of Good Hope, *C.Agardh collection 21490 A, B and C* (lecto-, here designated, LD).

NOTE

The original description does not indicate a type, neither does it mention a specimen that can be designated as holotype. Thus, we designated as lectotype C.Agardh's collection in Lund Herbarium 21490 A (male plant), B (tetrasporophyte), C (male plant) following Simons 1992 annotations.

Genus *Celeceras* Kützing

TYPE SPECIES. — *Celeceras monile* (Hooker & Harvey) Kützing.

REMARK

A valid name resurrected here because the type species *Celeceras monile* (Hooker & Harvey) Kützing, a synonym of *Ceramium puberulum* (Womersley 1978), is nested within this clade. These samples have 4-5 cortical initials with 2-3 descending filaments, tetrasporangia from periaxial cells, and are found only in the South Pacific.

KEY CHARACTERS

Terete to compressed thalli. Node formed by 6-10 periaxial cells cutting off 4-5 cortical initial cells with 2-3 descending filaments. Tetrasporangia formed by periaxial cells, 2-4 per node, partially covered by cortical cells to immersed in thalli, whorled, sometimes in stichidia-like.

*RbcL* alignment positions 522-546 5'TTCAATCGCTG-CAACAGGCCGAAGTG3' generated in this study.

*Celeceras novae-zelandiae* (J.Agardh)  
Barros-Barreto & Maggs, comb. nov.

*Microcladia novae-zelandiae* J.Agardh, *Lunds Universitets Årsskrift Andra Afdelningen, Kongl. Fysiografiska Sällskapet i Lund Handlingar* 33 (9): 35 (Agardh 1897).

TYPE LOCALITY. — **New Zealand**. South Island, Clair, Dunedin.

HOLOTYPE. — **New Zealand**. South Island, Clair, Dunedin, 25.XII.1896, J. C. Smith, *Herb. Agardh 21963* (holo-, LD[LD 2100380]).

*Celeceras pusilla* (Harvey)  
Barros-Barreto & Maggs, comb. nov.

*Ceramium pusillum* Harvey, *Phycologia Australica* 5: xlvii-xlviii (Harvey 1863).

TYPE LOCALITY. — **Australia**. Victoria, Port Fairy, 38°22'3.19"S, 142°15'26.62"E.

LECTOTYPE. — **Australia**. Victoria, Port Fairy, 38°22'3.19"S, 142°15'26.62"E, Harvey (lecto-, designated by Womersley [1978: 221], TCD[Herb. Harvey, Alg. Aust. Exsicc. 474D]).

ISOTYPE. — **Australia**. Victoria, Port Fairy, 38°22'3.19"S, 142°15'26.62"E (iso-, MEL[MEL 45330]).

Genus *Ceramium* Roth

*Ceramium glandulosum* (Solander ex Turner)  
Barros-Barreto & Maggs, comb. nov.

*Fucus glandulosus* Solander ex Turner, *Fuci sive generi a icones et historia*: 82, pl. 38 (Turner 1802).

*Microcladia glandulosa* (Solander ex Turner) Greville, *Algae britannicae* 1: 99 (Greville 1830).

LECTOTYPE. — Presumably **England**. S.l., s.d. (lecto-, designated by Maggs & Hommersand [1993], BM-K).

Genus *Herpochondria* F.Schmitz & Falkenberg

*Herpochondria borealis* (Ruprecht)  
Barros-Barreto & Maggs, comb. nov.

*Microcladia borealis* Ruprecht, *Algae Ochotenses*: 67 (Ruprecht 1850).

TYPE LOCALITY. — **United States**. Alaska, Unalaska.

LECTOTYPE. — **United States**. Alaska, Pinnacle, Summer Bay, Unalaska, 53°54'42.98"N, 166°27'16.99"E, *W.A. Setchell no. 5004* (lecto-, here designated, MICH[MICH 663173]; isolecto-, NY, WTU).

NOTE

Ruprecht did not designate a type in his publication. MICH 663173 (*W.A. Setchell no. 5004*) is designated as the lectotype as it was collected at the type locality Unalaska, Alaska, United States.

Genus *Pseudoceramium*  
Barros-Barreto & Maggs, gen. nov.

Terete plants with pseudodichotomous branching and forcipate tips, corticated at the nodes. Cortical development consisting of 7-10 periaxial cells cutting off four cortical initial cells; or cutting off two acropetal cells that laterally form a pseudoperiaxial cell; or two acropetal and two basipetal and a pseudoperiaxial cell. Tetrasporangia originating from periaxial cells uni- or bilaterally, forming 2-3 tetrasporangia covered by cortical cells.

TYPE SPECIES. — *Pseudoceramium oliveirarum* Barros-Barreto, Maggs & M.A.Jaramillo, sp. nov.

ETYMOLOGY. — From the Greek *pseudēs* meaning "false", referring to the pseudoperiaxial cell being cut off laterally from a periaxial cell but then observed in the ring of the periaxial cells.

*Pseudoceramium oliveirarum*

Barros-Barreto, Maggs & M.A.Jaramillo, gen. nov., sp. nov.

Plants mainly erect, 10-200 mm high, pseudodichotomously branched. Axes partially corticated, with apices strongly forcipate. Nodes formed by 8-9 periaxial cells each cutting off laterally 1-2 pseudoperiaxial cells. Periaxial cells also cut off two acropetal cells. Tetrasporangia formed by periaxial cells, unilateral/bilateral to verticillate, 1-3 per node, partially covered by cortical cells.

TYPE LOCALITY. — **Brazil**. Espírito Santo, Costão, Itapemirim.

HOLOTYPE. — **Brazil**. Espírito Santo, Costão, Itapemirim, 04.III.2004, *M. B. Barreto no. 47* (holo-, RB[RB 420029]).

GENBANK. — DQ458932 (*rbcL*), MW354756 (LSU), MW354770 (COI-5P).

ETYMOLOGY. — The epithet *oliveirarum* was chosen to honour Eurico Cabral de Oliveira Filho and Mariana Cabral de Oliveira, father and daughter who are exemplary Brazilian phycologists.

NOTES

This new species circumscribes a previously known taxon, widely distributed on the Brazilian coasts, usually identified as *Ceramium brevizonatum* var. *caraiibicum*. Detailed morphology and distribution are shown in Barros-Barreto & Yoneshigue-Valentin (2001) and Barros-Barreto *et al.* (2006). Its main morphological character is the node formed of 1-2 acropetal cells layers, 3-16 µm high, and periaxial cells cutting off 1-2 pseudoperiaxial cells 14-32 µm high. Axial cells are 60-140 µm in diameter and 42-142 µm high; 1-2 protruding unilateral tetrahedral tetrasporangia are partially covered by cortical cells 40-80 µm in diameter. This species is erected because it differs from *Ceramium brevizonatum* H.E.Petersen in having pseudoperiaxial cells and has a 3-4% genetic divergence for *rbcL*.

*Pseudoceramium brevizonatum* (H.E.Petersen)  
Barros-Barreto & Maggs, comb. nov.

*Ceramium brevizonatum* H.E.Petersen in Schmidt, *Report on the Danish Oceanographic expeditions 1908-1910 to the Mediterranean and adjacent seas* 2: 14, figs 8, 9 (Petersen 1918).

SYNTYPE LOCALITIES. — **Algeria**. Algiers.  
**France**. Menton.

SYNTYPES. — Silva *et al.* 1996: 390.

*Pseudoceramium caraiibicum* (H.E.Petersen & Børgesen)  
Barros-Barreto, Maggs & M.A.Jaramillo,  
comb. nov., stat. nov.

*Ceramium brevizonatum* var. *caraiibicum* H.E.Petersen & Børgesen in Børgesen, *Dansk Botanisk Arkiv* 4 (7): 29-30, fig. 11 (Børgesen 1924).

TYPE LOCALITY. — **Dominican Republic**. Beata Island (Silva *et al.* 1996: 391).

HOLOTYPE. — *Dansk Botanisk Arkiv* 4 (7): 30, fig. 11 (Børgesen 1924).

#### NOTES

This was morphologically characterized by Schneider (2004: figs 5-7) based on material from Bermuda, showing the nodal development and the presence of pseudoperiaxial cells. We chose a sequence (GenBank[AF259491]) from Yucatan, Mexico, to represent this species as it was obtained from close to the type locality, Honduras, and showed 3-4% genetic divergence (*rbcL*) from *Pseudoceramium brevizonatum* (H.E.Petersen) Barros-Barreto & Maggs, comb. nov. and *P. oliveirarum* Barros-Barreto, Maggs & M.A.Jaramillo, gen. nov., sp. nov.

*Pseudoceramium clarionense* (Setchell & N.L.Gardner)  
Barros-Barreto & Maggs, comb. nov.

*Ceramium clarionense* Setchell & N.L.Gardner, *Proceedings of the California Academy of Sciences*, Series 4, 19: 170, pl. 7, figs 25-27 (Setchell & Gardner 1930).

TYPE LOCALITY. — **Mexico**. Revillagigedo Archipelago, Isla Clarión.

HOLOTYPE. — **Mexico**. Revillagigedo Archipelago, Isla Clarión, VI.1925, *H.L. Mason no. 75* (holo-, CAS[CAS 173620]).

*Pseudoceramium inkyui* (T.O.Cho, Fredericq & S.M.Boo)  
Barros-Barreto & Maggs, comb. nov.

*Ceramium inkyui* T.O.Cho, S.Fredericq & S.M.Boo, *Journal of Phycology* 39: 237, figs 2-6 (Cho *et al.* 2003).

TYPE LOCALITY. — **South Korea**. Kyungju, on cliff below the lighthouse in Gampo.

HOLOTYPE (TETRASPOROPHYTE). — **South Korea**. Kyungju, on cliff below the lighthouse in Gampo, 8.IX.1999 (holo-, CNUK [CNUK c000215]).

*Pseudoceramium paniculatum* (Okamura)  
Barros-Barreto & Maggs, comb. nov.

*Ceramium paniculatum* Okamura, *Icones of Japanese algae* IV: 114, pl. 179, figs 8-16 (Okamura 1921).

TYPE LOCALITY. — **Japan**. Iwaki Province, Kamahara.

HOLOTYPE. — **Japan**. Iwaki Province, Kamahara, M. K. Nemoto (holo-, SAP[Herb. Okamura, Alg. Jap. Exsic. n. 2]!).

*Pseudoceramium planum* (Kützting)  
Barros-Barreto & Maggs, comb. nov.

*Ceramium planum* Kützting, *Species algarum*: 687 (Kützting 1849).

TYPE LOCALITY. — **South Africa**. Cape of Good Hope (Silva *et al.* 1996: 401).

LECTOTYPE. — **South Africa**. Cape of Good Hope (lecto-, designated by Kützting [1863: 5, pl. 11, figs C, D]).

*Pseudoceramium tenerrimum* (G.Martens)  
Barros-Barreto & Maggs, comb. nov.

*Ceramium tenerrimum* (G.Martens) Okamura, *Icones of Japanese Algae* IV: 112-114, pl. 179, figs 1-7 (Okamura 1921). — Basionym: *Hormoceras tenerrimum* G.Martens, *Die Tange. Die Preussische Expedition nach Ost-Asien. Nach Theil, Botanischer Theil*: 146, pl. VIII, fig. 2 (Martens 1868).

TYPE LOCALITY. — **Japan**. Nagasaki.

HOLOTYPE. — **Japan**. Nagasaki, IV.1861.

#### Genus *Reinboldiella* De Toni

*Reinboldiella filicula* (Harvey ex Womersley)  
Barros-Barreto & Maggs, comb. nov.

*Ceramium filiculum* Harvey ex Womersley, *Marine and Freshwater Research* 29 (2): 238, figs 4E, F, 15 A-E (Womersley 1978).

TYPE LOCALITY. — **Australia**. South Australia, Port Noarlunga.

HOLOTYPE. — **Australia**. South Australia, Port Noarlunga, in low eulittoral pools on offshore reef, on basal leaves of *Sargassum lacerifolium* (Turner) C.Agardh, 13.III.1977 (holo-, ADU[ADU A47978]).

#### Genus *Stirkia*

*Stirkia* Barros-Barreto & Maggs, gen. nov.

Thalli mainly erect, 10-200 mm high, consisting of irregularly branched axes with a wide variation in habit between species. Axes terete, partially to completely corticated, with apices straight to forcpate. Nodes formed by 6-8 periaxial cells each cutting off four cortical initials, two acropetal and two basipetal. Tetrasporangia formed by periaxial cells, unilateral/bilateral to verticillate, 1-3 per node, sometimes in stichidia-like groups immersed in the thalli. The *rbcL* alignment positions 696-709 5' GAACGATATGATCTT 3' generated in this study.

TYPE SPECIES. — *Stirkia fujiana* (Barros-Barreto & Maggs) Barros-Barreto & Maggs, comb. nov.

ETYMOLOGY. — The name *Stirkia* was chosen to honour Wendy A. Stirk, who worked on growth and morphogenesis of *Stirkia juliae* (A.Millar) Barros-Barreto & Maggs, comb. nov.

*Stirkia fujiana* (Barros-Barreto & Maggs)  
Barros-Barreto & Maggs, comb. nov.

*Ceramium fujianum* Barros-Barreto & Maggs, *Journal of Phycology* 42: 915-916, figs 9, 10 (Barros-Barreto *et al.* 2006).

TYPE LOCALITY. — **Brazil**. Espírito Santo, Enseada das Garças, Município Fundão.

HOLOTYPE (TETRASPOROPHYTE). — **Brazil**. Espírito Santo, Enseada das Garças, Município Fundão, 29.VII.2003 (holo-, RB[RB 420062]).



*Stirikia brasiliensis* (A.B.Joly)  
Barros-Barreto & Maggs, comb. nov.

*Ceramium brasiliense* A.B.Joly, *Boletim da Faculdade de Filosofia, Ciências e Letras, Universidade de São Paulo, Botânica* 14: 148, pl. 18, fig. 1A-D (Joly 1957).

TYPE LOCALITY. — **Brazil**. São Paulo State, Prainha, São Vicente.

HOLOTYPE. — **Brazil**. São Paulo State, Prainha, São Vicente, 20.VII.1955, *Joly 24-1955* (holo-, BM[BM000562289]).

*Stirikia codicola* (J.Agardh)  
Barros-Barreto & Maggs, comb. nov.

*Ceramium codicola* J.Agardh, *Lunds Universitets Årskrift, Andra Afdelningen, Kongl. Fysiografiska Sällskapet i Lund Handlingar* 30 (7): 23 (Agardh 1894).

*Ceramium codiophilum* Setchell & N.L.Gardner, *Proceedings of the California Academy of Sciences*, Series 4, 22: 89, pl. 8, figs 23, 24 (Setchell & Gardner 1937).

TYPE LOCALITY. — **United States**. California, Santa Cruz.

ISOTYPE. — **United States**. California, Santa Cruz, 36°58'40.0152"N, 122°1'20.244"W, *W. G. Farlow LD 20930* (iso-, designated by Cho *et al.* [2002: 557], UC[UC1859260]).

*Stirikia coulteri* (Harvey)  
Barros-Barreto & Maggs, comb. nov.

*Microcladia coulteri* Harvey, *Smithsonian Contributions to Knowledge* 5 (5): 209, pl. XXXIII, fig. A (Harvey 1853).

TYPE LOCALITY. — **United States**. California, Monterey.

LECTOTYPE. — **United States**. California, Monterey, 1853, Thomas Coulter, *Thomas s.n.* (lecto-, here designated, TCD[TCD 0012510]; syn-, NY[NY 02221008]) (Wallace 2019).

NOTE

*RbcL* alignment positions 696-709 5'AAACGATATGATCTT3' generated in this study.

*Stirikia dumoserta* (R.E.Norris & I.A.Abbott)  
Barros-Barreto & Maggs, comb. nov.

*Ceramium dumosertum* R.E.Norris & I.A.Abbott, *Pacific Science* 46 (4): 456 (Norris & Abbott 1992).

TYPE LOCALITY. — **United States**. Hawai'i, Maui Island, intertidal on basalt, Ka'inalimu Bay, Hana.

HOLOTYPE. — **United States**. Hawai'i, Maui Island, intertidal on basalt, Ka'inalimu Bay, Hana, 21.VII.1990, legit *I.A. Abbott 20307* (holo-, BISH[BISH 612652]).

*Stirikia horrida* (Setchell & N.L.Gardner)  
Barros-Barreto & Maggs, comb. nov.

*Ceramium horridum* Setchell & N.L.Gardner, *Proceedings of the California Academy of Sciences*, Series 4, 12: 777, pl. 26, figs 49, 50, pl. 79 (Setchell & Gardner 1924).

TYPE LOCALITY. — **Mexico**. Sonora, Guaymas.

HOLOTYPE. — **Mexico**. Sonora, Guaymas, V.1917, *Marchant no. 91* (holo-, UC[UC1462246]).

*Stirikia interrupta* (Setchell & N.L.Gardner)  
Barros-Barreto & Maggs, comb. nov.

*Ceramium interruptum* Setchell & N.L.Gardner, *Proceedings of the California Academy of Sciences*, Series 4, 12: 775, pl. 27, fig. 58 (Setchell & Gardner 1924).

TYPE LOCALITY. — **United States**. California, Eureka, near La Paz.

HOLOTYPE. — **United States**. California, Eureka, near La Paz, V.1917, *Marchant no. 78* (holo-, UC).

*Stirikia japonica* (Okamura)  
Barros-Barreto & Maggs, comb. nov.

*Ceramium japonicum* Okamura, *Botanical Magazine, Tokyo* 10 (110-111): 38, pl. 3, figs 24-28 (Okamura 1896).

TYPE LOCALITY. — **Japan**. Noto.

HOLOTYPE. — **Japan**. Noto (holo-, SAP[Okamura collection Alg. Jap. Exsic.]).

NOTE

*RbcL* alignment positions 696-709 5'GAATGATATGATCTT3' generated in this study.

*Stirikia juliae* (A.Millar)  
Barros-Barreto & Maggs, comb. nov.

*Ceramium juliae* A.Millar, *Australian Systematic Botany* 15: 494, figs 1-12 (2002).

TYPE LOCALITY. — **Australia**. New South Wales, Honeysuckle Point, Twofold Bay.

HOLOTYPE. — **Australia**. New South Wales, Honeysuckle Point, Twofold Bay, 15 m deep, 37°05'57"S, 149°56'21"E, 4.II.1992, *A. Millar s.n.* (holo-, NSW[NSW605422], slide 12-97).

*Stirikia pacifica* (Collins)  
Barros-Barreto & Maggs, comb. nov.

*Ceramium pacificum* (Collins) Kylin, *Lunds Universitets Årskrift, Ny Följä, Andra Afdelningen* 21 (9): 65 (Kylin 1925). — Basionym: *Ceramium rubrum* var. *pacificum* Collins, *Geological Survey. Victoria Memorial Museum, Bulletin* 1: 125 (Collins 1913).

*Ceramium washingtoniense* Kylin, *Lunds Universitets Årsskrift, Ny Följd, Andra Afdelningen* 21 (9): 62 (Kylin 1925). — Type: **United States**. Washington, False Bay, San Juan Island, 24.VII.1924, H. Kylin (LD[LD 1265409]).

TYPE LOCALITY. — **United States**. Monterey, California (Cho *et al.* 2002: 565).

LECTOTYPE. — **United States**. Monterey, California (lecto-, designated by Cho *et al.* [2002: 565], FH).

*Stirkia sinicola* (Setchell & N.L.Gardner)  
Barros-Barreto & Maggs, comb. nov.

*Ceramium sinicola* Setchell & N.L.Gardner, *Proceedings of the California Academy of Sciences*, Series 4, 12: 773, pl. 25, figs 40, 41, pl. 75 (Setchell & Gardner 1924).

TYPE LOCALITY. — **Mexico**. Baja California, Ensenada Bay.

HOLOTYPE. — **Mexico**. Baja California, Ensenada Bay, 7.IV.1921, *Ivan M. Johnston no. 67b* (holo-, UC[UC1859340]).

*Stirkia vaga* (P.C.Silva)  
Barros-Barreto & Maggs, comb. nov.

*Ceramium vagans* P.C.Silva, *Smithsonian Contributions to Marine Sciences* 27: 56 (Silva *et al.* 1987).

*Ceramium vagabundum* E.Y.Dawson, nom illeg., *Pacific Science* 11: 121, fig. 27E (as “vagabunde”) (Dawson 1957).

TYPE LOCALITY. — **Marshall Islands**. Eniwetok Atoll, Parry Island.

HOLOTYPE. — **Marshall Islands**. Eniwetok Atoll, Parry Island, 19.VIII.1955, *Dawson no. 13620a* (holo-, BISH).

Genus *Yoneshiguela*  
Barros-Barreto, Maggs & M.A.Jaramillo, gen. nov.

Thalli terete with straight apices. Node formed by 4-6 periaxial cells cutting off two acropetal cells. Tetrasporangia formed by periaxial cells, 1-3 per node, naked or partially covered by cortical cells; tetrasporangia unilateral to bilateral (Fig. 1E, K, O).

TYPE SPECIES. — *Yoneshiguela affinis* (Setchell & Gardner) Barros-Barreto, Maggs & M.A.Jaramillo, comb. nov.

ETYMOLOGY. — The name was selected to honour a pioneering female Brazilian phycologist, Yocie Yoneshigue-Valentin.

*Yoneshiguela affinis* (Setchell & N.L.Gardner)  
Barros-Barreto, Maggs & M.A.Jaramillo, comb. nov.

*Ceramium affine* Setchell & N.L.Gardner, *Proceedings of the California Academy of Sciences*, Series 4, 19: 172 (Setchell & Gardner 1930).

TYPE LOCALITY. — **Mexico**. Baja California, Isla Guadalupe.

HOLOTYPE. — **Mexico**. Baja California, Isla Guadalupe, 25.IV.1924, *H.L. Mason no. 36*, (holo-, UC[UC2056026]).

GENBANK. — DQ458920 (*rbcL*), MW354769 (COI-5P).

*Yoneshiguela compta* (Børgesen)  
Barros-Barreto, Maggs & M.A.Jaramillo, comb. nov.

*Ceramium comptum* Børgesen, *Dansk Botanisk Arkiv* 4 (7): 28-29, fig. 10 (Børgesen 1924).

TYPE LOCALITY. — **Dominican Republic**. Beata Island (Silva *et al.* 1996: 393).

HOLOTYPE. — *Dansk Botanisk Arkiv* 4 (7): 29, fig. 10 (Børgesen 1924).

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## APPENDICES

## APPENDIX 1. — Nomenclatural history of genera of Ceramieae C.Agardh ex Greville.

The genus *Ceramium* Roth currently includes the great majority of species in the Ceramieae (Table 1), but its circumscription is problematic, partly due to morphological plasticity (Garbary *et al.* 1978; Maggs *et al.* 2002; Wolf *et al.* 2011). *Ceramium* has been divided several times into series or subgenera. Various genera (Table 2) have been segregated from *Ceramium* using characters such as tetrasporangial position, nodal cortication, and spine characters that may vary even within species (Table 1; Maggs & Hommersand 1993). In 1842 and 1849, Kützing described *Hormoceras*, *Gongroceras*, *Trichoceras*, *Echinoceras*, *Celeceras*, *Acanthoceras*, and *Pteroceras*, but these have always been regarded as synonyms of *Ceramium* (Table 2). Agardh (1894) grouped *Ceramium* into three series, *Ectoclinia*, *Dichoclinia* and *Periclinia* and 16 tribes that do not have correspondence with previously recognized groupings, based mostly on the position of tetrasporangia. Nakamura (1950, 1954, 1965) later subdivided *Ceramium* by the degree of cortication into the subgenera *Hormoceras* (Kützing) Nakamura, *Mesoceramium* Nakamura, and *Euceramium* De Toni.

*Centroceras* Kützing (1841) was segregated from *Ceramium* because cortical cells are in regular longitudinal rows (Norris 1993). Although its distinctness has been questioned (Simons 1968; Itono 1977) in molecular analyses, *Centroceras* species form a well-resolved clade related to *Gayliella* (Barros-Barreto *et al.* 2006; Cho *et al.* 2008a; Won *et al.* 2009; Schneider *et al.* 2015; Gomes *et al.* 2020). Furthermore, male reproductive structures (spermatangia) originate from periaxial cells uniquely in *Centroceras* (Hommersand 1963; Table 1).

*Corallophila* Weber van Bosse (1923) is another segregate genus, based on the poorly known Indonesian species *Corallophila kleiwegii* Weber van Bosse. Norris (1993) considered the diagnostic characters of *Corallophila* to be its prostrate habit, complete cortication, and basipetal growth of corticating filaments and transferred to it several species of *Centroceras*, *Ceramium*, and *Ceramiella*. This extended the range of *Corallophila* to the Atlantic Ocean, the Mediterranean Sea, and the Hawaiian Islands. *Ceramium eatonianum* from California was later transferred to *Corallophila* on morphological grounds (Cho *et al.* 2000), and molecular phylogenetic analyses confirmed that it was not closely related to other *Ceramium* species (Barros-Barreto *et al.* 2006; Cho *et al.* 2008a).

The type species of *Campylaephora* Agardh (1851) is *C. hypnaeoides*, a Japanese species with a thick cortex and sickle-shaped branch endings (Table 1). The main characters of this genus are the presence of true rhizoidal filaments in the cortex (Schmitz & Hauptfleisch 1897) and a discoid holdfast (Nakamura 1954). These diagnostic characters of *Campylaephora* have been questioned (e.g. Boo & Yoshida 1991; Boo &

Lee 1994), but molecular studies supported its recognition (Cho *et al.* 2008b). The key character was considered to be the formation of secondary pit connections from the rhizoidal filaments (Cho *et al.* 2008b).

*Microcladia* Greville (1830) has compressed axes and planar branching (Table 1). The type specimen of the type species *M. glandulosa* is from England (north-east Atlantic), and *M. glandulosa* is known from Atlantic and Mediterranean coasts of Europe, but the other members are Pacific or Southern Hemisphere (Hommersand 1963; Maggs & Hommersand 1993).

*Herpochondria* was at one time considered a synonym of *Microcladia* (Okamura 1900) but later resurrected (Weber van Bosse 1923; Kylin 1956). The diagnostic characters, prostrate vs erect thallus (in *Herpochondria* vs *Microcladia*, respectively) and the sequence of periaxial cell formation, two lateral and four transverse (Itono 1977), differentiate these genera. However, other authors consider these characteristics inadequate for generic delimitation (Hommersand 1963; Wynne 1985b).

*Carpoblepharis*, with which *Reinboldiella* has sometimes been placed in synonymy (Lin & Hommersand 2007), has compressed axes and planar branching (Table 1), and its distribution is restricted to the Southern Hemisphere, Florida (United States) and South Africa, and NW Pacific. *Reinboldiella* (De Toni 1895; Okamura 1900; Yoshida 1998) species can be distinguished from *Carpoblepharis* by their smaller size and repent habit (Feldmann & Mazoyer 1937; Hommersand 1963) and rosette-like (Suzuki & Lin 2017) membranous blades, epiphytic on benthic red algae, with a wide distribution in the north-western Pacific Ocean (Taiwan, Korea and Japan). The type species *Reinboldiella schmitziana* has been recognized as *Carpoblepharis schmitziana* var. *erecta* Okamura. *Reinboldiella warburgii* (Heydrich) Yoshida & Mikami in Yoshida 1998 (formerly known as *Carpoblepharis warburgii* Heydrich) occurs only in NW Pacific.

*Gayliella* T.O.Cho, L.J.McIvor & S.M.Boo was segregated from *Ceramium* for its unicellular rhizoids and unique cortical development that forms only one basipetal cell (Fig. 1F, L; Table 1; Cho *et al.* 2008a). In molecular and integrative analyses, members of this genus form a well-resolved clade that consists of 15 species (Barros-Barreto *et al.* 2006; Cho *et al.* 2008a).

*Ardreanema* is a morphologically distinct monotypic genus from the Pacific Ocean (Table 1), and two tiny and poorly known parasitic genera, *Syringocolax* Reinsch and *Centrocerocolax* A.B.Joly, are not considered further here.

Molecular analyses led to the segregation of *Gayliella* from *Ceramium* and confirmed the polyphyly of the remainder of the genus *Ceramium* (Barros-Barreto *et al.* 2006; Cho *et al.* 2008a).



APPENDIX 2. — Sample information and GenBank accession number. Abbreviations: **CAM**, Christine A. Maggs; **LM**, Lynne McIvor; **MBBB**, M.B. Barros-Barreto; **MHH**, Max Hommersand.

Sample	Herbaria/ GenBank names	Sample number	Location and specimen voucher	Date collected	Collector	GenBank accession number		
						<i>rbcL</i>	Partial LSU	COI-5P
<i>Campylaephora borealis</i> (Y.Nakamura) K.S.Seo, T.O.Cho & S.M.Boo	–	–	South Korea: Sinnam, Kangwon	25.II.1998	T.O. Cho & H.S. Yoon	AY945767	DQ238798	–
<i>Campylaephora boydenii</i> (E.S.Gepp) Barros-Barreto & Maggs, comb. nov.	<i>Ceramium boydenii</i> E.S.Gepp	CAM 412	Japan: Uranohama. NCU-A-0004403	11.IX.1994	MHH	MW366520	–	–
<i>Campylaephora californica</i> (Farlow) T.O.Cho in T.O.Cho, Hommersand, B.Y.Won & Fredericq	–	CAM 409	USA: Pigeon Point, San Mateo Co, California. NCU-A-0003395	21.XII.1992	MHH	MW366519	–	–
<i>Campylaephora californica</i>	–	TC395	USA: California, Pigeon Point, San Mateo Co	21.XII.1992	MHH	EF613500	–	–
<i>Campylaephora californica</i>	–	AC274	USA: California, Monterey	7.IX.2006	A. L. Carlile	GQ252449	–	–
<i>Campylaephora crassa</i> (Okamura) Nakamura	–	–	South Korea: Sinnam, Kangwon	25.II.1998	T.O. Cho & H.S. Yoon	AY945769	–	–
<i>Campylaephora gardneri</i> (Kylin) Barros-Barreto & Maggs, comb. nov.	<i>Ceramium gardneri</i> Kylin	AC247	USA: San Juan Is., Washington	2.VIII.2006	–	GQ252455	–	–
<i>Campylaephora gardneri</i>	<i>Ceramium gardneri</i>	AC307	USA: San Juan Is., Washington	2.VIII.2007	–	GQ252456	–	–
<i>Campylaephora gardneri</i>	<i>Ceramium gardneri</i>	AC311	USA: San Juan Is., Washington	5.VIII.2007	–	GQ252457	–	–
<i>Campylaephora hypnaeoides</i> J.Agardh	–	–	South Korea: Daesado, Wando	13.VI.1999	T.O. Cho & W.J. Lee	EF613506	–	–
<i>Campylaephora hypnaeoides</i>	–	–	Japan: Akkeshi, Hokkaido	7.V.1999	S.M. Boo & H.S. Yoon	EF613505	–	–
<i>Campylaephora hypnaeoides</i>	–	–	Japan: Sonohora, Tsuyazaki, Fukuoka	18.III.1999	T.O. Cho & S.P.W. Kawaguchi	–	DQ238797	–
<i>Campylaephora kondoi</i> (Yendo) Barros-Barreto & Maggs, comb. nov.	<i>Ceramium kondoi</i> Yendo	C163	Japan: Hokkaido, Akkeshi	–	–	AY770641	–	–
<i>Campylaephora kondoi</i>	<i>Ceramium kondoi</i>	C554	South Korea: Taeon, Bangpo	–	–	AY770638	–	–
<i>Campylaephora kondoi</i>	<i>Ceramium kondoi</i>	AC230	South Korea: Yeosu, Anpori	16.V.2006	–	GQ252460	–	–
<i>Campylaephora kondoi</i>	<i>Ceramium kondoi</i>	–	South Korea: Taeon, Hakampo	–	E.C. Yang & S.M. Boo	AY295176	–	–
<i>Campylaephora kondoi</i>	<i>Ceramium kondoi</i>	–	South Korea: Namhae, Kyengnam	30.III.1998	T.O. Cho	–	DQ238804	–
<i>Campylaephora kondoi</i>	<i>Ceramium kondoi</i>	mbccc09	China, Qingdao Huiquan Bay	III.2011	–	–	–	JQ619158
<i>Campylaephora kondoi</i>	<i>Ceramium kondoi</i>	C1318	Japan: Aomori, Senjoujiki	–	–	DQ350384	–	–
<i>Campylaephora kondoi</i>	<i>Ceramium kondoi</i>	LQDHQW2011 1124-R21	China	11.XI.2011	Wu F.-F.	–	KC795847	–
<i>Campylaephora sungminbooi</i> (J.R.Hughey & G.H.Boo) Barros- Barreto & Maggs, comb. nov.	<i>Ceramium sungminbooi</i>	–	Norway: Frognerkilen, Oslofjord	5.IX.1996	Jan Rueness	KX037019	–	–
<i>Campylaephora sungminbooi</i>	<i>Ceramium sungminbooi</i>	–	South Korea: Hoedong, Jindo. CNUK 034423	28.II.2002	–	KU160485	–	–
<i>Campylaephora sungminbooi</i>	<i>Ceramium</i> sp.	AC239	South Korea: Taeon, Magumpo	26.V.2006	–	GQ252466	–	–
<i>Campylaephora</i> sp. 1	<i>Campylaephora</i> sp.	OSsj0609-7	South Korea	9.VI.2017	–	MH200825	–	–
<i>Campylaephora</i> sp. 2	–	LM 1554	Japan: East Sagami Bay BM (NH)	12.VII.2003	C. Trowbridge	MW366526	–	–

APPENDIX 2. — Continuation.

Sample	Herbaria/ GenBank names	Sample number	Location and specimen voucher	Date collected	Collector	GenBank accession number		
						<i>rbcL</i>	Partial LSU	COI-5P
<i>Campylocephora</i> sp. 3	<i>Ceramium cimbricum</i> H.E.Petersen in Rosenvinge	AC177	USA: Sitka, Alaska	22.V.2005	–	<a href="#">GQ252452</a>	–	–
<i>Campylocephora</i> sp. 3	<i>Ceramium cimbricum</i>	AC185	USA: Sitka, Alaska	24.VI.2005	–	<a href="#">GQ252453</a>	–	–
<i>Campylocephora</i> sp. 4	<i>Ceramium californicum</i> J.Agardh	TC006	USA: Oregon, Yaquina Bay	13.VII.1998	T.O. Cho & G.-I. Hansen	<a href="#">AY591931</a>	–	–
<i>Campylocephora</i> sp. 4	<i>Ceramium californicum</i>	AC279	USA: Cape Arago, Oregon	14.VI.2007	–	<a href="#">GQ179819</a>	–	–
<i>Carpoblepharis flaccida</i> (J.V.Lamouroux) Kützing	–	ODC 855	South Africa: Kommetjie, Western Cape Province	9.XI.1999	ODC	<a href="#">AY945764</a>	–	–
<i>Carpoblepharis flaccida</i>	–	–	South Africa	–	–	<a href="#">DQ787567</a>	–	–
<i>Carpoblepharis flaccida</i>	–	CUK14732	South Africa: Hout Bay Harbour Cape Town Western Cape	–	–	–	–	<a href="#">MH251749</a>
<i>Carpoblepharis minima</i> E.S.Barton	–	Lynn1561	South Africa	–	LM	<a href="#">MW366505</a>	–	–
<i>Carpoblepharis minima</i>	–	TC408	Namibia: Grossbuchte, Luderitz	9.VII.1993	MHH	<a href="#">EF613508</a>	–	–
<i>Carpoblepharis obsoleta</i> (C.Agardh) Barros-Barreto & Maggs, comb. nov.	<i>Ceramium obsoletum</i> C.Agardh	CAM 1056	South Africa: Hout Bay, Cape Town	24.XI.1999	ODC	<a href="#">FR871402</a>	–	–
<i>Carpoblepharis</i> sp.	<i>Ceramium</i> sp. 3	CAM 414	USA: Washington, Puget Sound, Neah Bay	11.VI.1994	MHH	<a href="#">FR871406</a>	–	–
<i>Celeceras monile</i> (Hooker & Harvey) Kützing	<i>Ceramium puberulum</i> Sonder	–	Port MacDonnell, Discovery Bay, South Australia. NCU-A-0004649	28.VIII.1995	MHH	<a href="#">MW366517</a>	–	–
<i>Celeceras novae-zelandiae</i> (J.Agardh) Barros-Barreto & Maggs, comb. nov.	<i>Microcladia novae-zelandiae</i> J.Agardh	CAM 411	New Zealand: Aromoana. BM000701861	29.III.1994	W. Nelson via MHH	<a href="#">MW366518</a>	–	–
<i>Celeceras pusilla</i> (Harvey) Barros- Barreto & Maggs, comb. nov.	<i>Ceramium pusillum</i> Harvey	CAM 1542	New Zealand: Christchurch	I.2003	M.P. Johnson	<a href="#">FR871403</a>	–	–
<i>Centroceras arcii</i> C.W.Schneid., Popolizio & C.E.Lane	–	CWS/CEL09- 13-6	Bermuda: Horseshoe Bay	16.III.2009	C.W. Schneider & C.E. Lane	<a href="#">KP222800</a>	–	–
<i>Centroceras arcii</i>	–	BDA 0870	Bermuda: Devonshire Bay	16.II.2012	T.R. Popolizio	–	–	<a href="#">KP222761</a>
<i>Centroceras clavulatum</i> (C.Agardh) Montagne	–	–	Peru: Punta La Cruz, Ancon, Lima	30.VIII.2003	N. Arakaki	–	<a href="#">DQ374363</a>	–
<i>Centroceras clavulatum</i>	–	C76	South Korea: Pohang, Guryongpo	7.VII.1999	E.C. Yang & Boo S.M	–	–	<a href="#">EU194971</a>
<i>Centroceras gasparrinii</i> (Meneghini) Kützing	<i>Centroceras clavulatum</i>	MBBB 48	Brazil: Mangue, Itapemirim, Espírito Santo. RB420016	4.III.2004	MBBB	<a href="#">DQ458919</a>	<a href="#">MW354752</a>	–
<i>Centroceras gasparrinii</i>	–	MBBB 143	Brazil: Praia da Joana, Rio das Ostras, Rio de Janeiro. RB420072	26.VIII.2005	MBBB	–	<a href="#">MW354751</a>	<a href="#">MW354765</a>
<i>Centroceras gasparrinii</i>	–	MBBB 526	Brazil: Praia de Manguinhos, Armação de Búzios, Rio de Janeiro. R232586	21.VIII.2013	MBBB	<a href="#">MW366535</a>	<a href="#">MN105062</a>	<a href="#">MN105048</a>

## APPENDIX 2. — Continuation.

Sample	Herbaria/ GenBank names	Sample number	Location and specimen voucher	Date collected	Collector	GenBank accession number		
						<i>rbcL</i>	Partial LSU	COI-5P
<i>Centroceras gasparrinii</i>	–	B6	Brazil: Praia Rasa, Buzios, RJ	22.XI.2003	C.F.D. Gurgel	DQ374311	DQ374349	–
<i>Centroceras gasparrinii</i>	–	LM 1559	Morocco: Devil's Point; culture. BM000701866	II.2002	CAM	AF439294	–	–
<i>Centroceras gasparrinii</i>	–	–	South Korea: Gampo, Pohang	27.IX.1998	T.O. Cho & H.S. Yoon	AY945766	–	–
<i>Centroceras gasparrinii</i>	<i>Centroceras minutum</i> Yamada	–	Australia: Horn Island, Queensland	21.VI.2002	–	DQ374321	–	–
<i>Centroceras gasparrinii</i>	–	–	South Africa: Reunion Rocks, KwaZulu-Nata	17.VIII.2005	T.O. Cho & S. Fredericq	DQ374320	–	–
<i>Centroceras gasparrinii</i>	–	BDA 0356	Bermuda: St. George's Harbour	23.VIII.2010	C.W. Schneider & C.E. Lane	KP222805	–	KP222745
<i>Centroceras gasparrinii</i>	–	TC6721	South Korea: Jindo, Baekdongri, Imhoemyeon	16.IV.2001 20.VIII.2009	T.O. Cho, S.Y. Jeong & J.K. Lee	HM240515	–	–
<i>Centroceras gasparrinii</i>	<i>Centroceras clavulatum</i>	ARS02604	US: Hawaii	–	–	–	HQ422498	–
<i>Centroceras gasparrinii</i>	<i>Centroceras clavulatum</i>	ARS03547	US: Hawaii	–	–	–	HQ422061	–
<i>Centroceras gasparrinii</i>	<i>Centroceras clavulatum</i>	ARS03696	US: Hawaii	–	–	–	HQ422191	–
<i>Centroceras gasparrinii</i>	<i>Centroceras clavulatum</i>	ARS03255	US: Hawaii	–	–	–	HQ422016	–
<i>Centroceras gasparrinii</i> (Meneghini) Kützing subsp. <i>minor</i> M.A.Wolf, A.Buosi, A.S.Juhmani & A.Sfriso	<i>Centroceras gasparrinii</i>	A000838	Italy: Venice	–	–	LR536401	–	–
<i>Centroceras hommersandii</i> Won, T.O.Cho & Fredericq	–	B105	South Africa: Trafalgar, KwaZulu-Nata	20.II.1999	E. Coppejans <i>et al.</i>	DQ374322	–	–
<i>Centroceras hyalacanthum</i> Kützing	–	TC524	USA: Florida, Nerritt Island, Brevard Co., E. Florid	5.III.2003	T.O. Cho & B.Y. Won	DQ374341	DQ374366	–
<i>Centroceras hyalacanthum</i>	–	BDA 0590	Bermuda: Cove east of Spanish Pt.	18.I.2012	C.W. Schneider & C.E. Lane	KP222803	–	KP222789
<i>Centroceras hyalacanthum</i>	–	ARS02737	USA: Hawaii, Oahu	–	–	–	HQ422526	–
<i>Centroceras illaqueans</i> C.W.Schneider, Cianciola & Popolizio	–	BDA 09-2-9	Bermuda: Capt. William's Bay	15.III.2009	C.W. Schneider & C.E. Lane	KP222802	–	KP222781
<i>Centroceras micracanthum</i> Kützing	–	W01063	Panama: Galeta Island, Smithsonian Tropical Research Institute (STRI), Caribbean entrance to the Panama Canal	1.X.1999	B. Wysor	DQ374336	DQ374365	–
<i>Centroceras micracanthum</i>	–	BDA 0584	Bermuda: Cove east of Spanish Pt.	18.I.2012	C.W. Schneider	KP222804	–	KP222770
<i>Centroceras natalense</i> Won, T.O.Cho & Fredericq	–	TC2796	South Africa: Leisure Bay	24.VIII.2005	T.O. Cho & S. Fredericq	DQ374343	–	–
<i>Centroceras rodmanii</i> Won, T.O.Cho & Fredericq	–	TC435	Chile: Cocholgue, Bahia Concepcion	1.I.1996	MHH	DQ374333	DQ374364	–
<i>Centroceras tetrachotomum</i> Won, T.O.Cho & Fredericq	–	TC415	South Africa: Lambert Bay, Western Cape	25.I.2001	MHH	DQ374323	DQ374360	–

APPENDIX 2. — Continuation.

Sample	Herbaria/ GenBank names	Sample number	Location and specimen voucher	Date collected	Collector	GenBank accession number		
						<i>rbcL</i>	Partial LSU	COI-5P
<i>Centroceras</i> sp. 1	<i>Centroceras clavulatum</i>	–	Jamaica: Falmouth, Trelawny Province	VII.1999	D.T. Thomas	DQ022809	–	–
<i>Centroceras</i> sp. 2	<i>Centroceras</i> sp. 1	HV06148	Australia: VIC, Mallacoota	–	Heroen Verbruggen & Kyatt Dixon	MK125359	–	–
<i>Centroceras</i> sp. 3	<i>Centroceras</i> sp. 3	HV06015	Australia: VIC, Mallacoota	–	Heroen Verbruggen & Kyatt Dixon	MK125362	–	–
<i>Centroceras</i> sp. 4	<i>Centroceras clavulatum</i>	AC272	USA: CA, Monterey	7.IX.2006	–	GQ252451	–	–
<i>Centroceras</i> sp. 5	<i>Centroceras</i> sp. 1	1Tris	UK: Tristan da Cunha, Saint Helena: Nightingale. Nightingale 2010 024	21.III.2010	Sue Scott	MK185797	–	MK202400
<i>Centroceras</i> sp. 6	<i>Centroceras</i> sp. 1	1Tris	UK: Tristan da Cunha, Saint Helena: West of Harbour. Pools 2010 069	31.III.2010	Sue Scott	–	–	MK202411
<i>Centroceras</i> sp. 7	–	ARS03786	USA: Hawaii, Oahu	19.IV.2008	A. Kurihara	–	–	HQ422953
<i>Centroceras</i> sp. 8	<i>Centroceras clavulatum</i>	GWS015026	Australia	19.I.2010	G.W. Saunders & K. Dixon	–	–	HM917544
<i>Centroceras</i> sp. 9	<i>Centroceras clavulatum</i>	GWS021277	USA: California, Pigeon Point Lighthouse	15.V.2010	B. Clarkston & K. Hind	–	–	KM254257
<i>Ceramium barbatum</i> Kützinger	–	CAM 1528	Italy: Lerici, Liguria. BM000701867	11.VII.2001	CAM	FR871396	–	–
<i>Ceramium botryocarpum</i> A.W.Griffiths ex Harvey	–	CAM 275	N. Ireland: Annalong, Co. Down	XI.1993	CAM	AF439288	–	–
<i>Ceramium botryocarpum</i>	–	CAM 1081	N. Ireland: Annalong, Co. Down	25.I.2003	CAM	–	MW354748	MW354764
<i>Ceramium ciliatum</i> (Ellis) Ducluzeau	–	GALW	Ireland: Finavarra, Co. Clare	2003	L.M. GALW	FR871397	–	–
<i>Ceramium ciliatum</i>	–	strain 25996	Spain: Tragove, Pontevedra	4.III.2011	Javier Cremades	–	–	KJ179929
<i>Ceramium cimbricum</i> H.E.Petersen in Rosenvinge	–	CAM 211	Ireland: Tamney, Mulroy Bay, Donegal. BM000701865 (Maggs & Hommersand 1993: fig 15b)	15.II.1993	CAM	MW366531	–	–
<i>Ceramium cimbricum</i>	–	CAM 212	Ireland: Tamney, Mulroy Bay, Donegal. BM000701863	15.II.1993	CAM	MW366532	–	–
<i>Ceramium cimbricum</i>	–	C 8843/C-A- 37605	Denmark: Egerslev Ron, Limfjorden	27.VII.1920	H. Petersen	KU925350	–	–
<i>Ceramium circinatum</i> (Kützinger) J.Agardh	–	CAM 181	England: Kimmeridge, Dorset	13.X.1992	CAM	FR871398	–	–
<i>Ceramium connivens</i> Zanardini	–	–	Italy: Ca' Roman, Pellestrina	–	–	LR031254	–	–
<i>Ceramium derbesii</i> Solier ex Kützinger	–	#4 (HA 3150-1)	Venice Lagoon, Lido di Venezia, Italy	VI.2010	Wolf & Sciuto	FR775778	–	–



## APPENDIX 2. — Continuation.

Sample	Herbaria/ GenBank names	Sample number	Location and specimen voucher	Date collected	Collector	GenBank accession number		
						<i>rbcL</i>	Partial LSU	COI-5P
<i>Ceramium deslongchampsii</i> Chauvin ex Duby	–	CAM 45	N. Ireland: Helen's Bay, Co. Down	30.III.1992	CAM	<a href="#">AF439293</a>	–	–
<i>Ceramium diaphanum</i> (Lightfoot) Roth	–	NCweed1220	USA: North Carolina, Onslow Bay, Atlantic Ocean, Wynne Plaza Park	18.III.2013	DW Freshwater	–	–	<a href="#">KF367755</a>
<i>Ceramium diaphanum sensu</i> Harvey	–	CAM 199	England: Cornwall,	10.III.1993	CAM	<a href="#">FR871401</a>	–	–
<i>Ceramium</i> aff. <i>diaphanum</i>	–	CAM 249	Canada: Pomquet Harbour, Antigonish Co., Nova Scotia	26.IX.1993	C. Bird	<a href="#">FR871400</a>	–	–
<i>Ceramium</i> aff. <i>diaphanum</i>	–	CAM 136	Ireland: St John's Point, West Donegal	29.VIII.1992	CAM	<a href="#">FR871399</a>	–	–
<i>Ceramium echionotum</i> J.Agardh	–	LM 1027	Canary Islands: Callejo, Fuerteventura	25.III.1999	CAM	<a href="#">AF439313</a>	–	–
<i>Ceramium echionotum</i>	–	RMAR2945	France: Brittany, Le Loup	30.VIII.2011	Couceiro L. & Robuchon M.	–	–	<a href="#">KJ960509</a>
<i>Ceramium gaditanum</i> (Clemente) Cremades	–	CAM 1052	UK: Broad Haven, Pembrokeshire, Wales. BM013821504	18.III.2000	CAM	<a href="#">MW366534</a>	–	–
<i>Ceramium gaditanum</i>	–	MBBB 64	Spain: Cudillero, Asturias.	20.I.2005	CAM	–	<a href="#">MW354753</a>	–
<i>Ceramium glandulosum</i> (Solander ex Turner) Barros-Barreto & Maggs, comb. nov.	<i>Microcladia glandulosa</i> (Solander ex Turner) Greville	CAM 322	England: Helston, Cornwall BM(NH)	30.VII.1994	CAM	<a href="#">MW366533</a>	–	–
<i>Ceramium nodosum</i> (Kützing) A.W.Griffiths & Harvey	–	–	Italy: Ca' Roman, Pellestrina	–	–	<a href="#">LR031256</a>	–	–
<i>Ceramium nudiusculum</i> (Kützing) Rabenhorst	–	#2 (HA 3150-4)	Venice Lagoon, Lido di Venezia, Italy	VI.2010	Wolf & Sciuto	<a href="#">FR775780</a>	–	–
<i>Ceramium pallidum</i> (Kützing) Maggs & Hommersand	–	CAM 223	Ireland: Flannery's Bridge, Kilkieran Bay, Co. Galway	12.VI.1993	CAM	<a href="#">AF439292</a>	–	–
<i>Ceramium pallidum</i>	–	GWS039884	Norway: Ormhilleren (site 1)	5.VI.2016	G.W. Saunders & T. Bringloe	<a href="#">MN184533</a>	–	<a href="#">MN184264</a>
<i>Ceramium pallidum</i>	–	GWS039872	Norway: Hellesoy	5.VI.2016	G.W. Saunders & T. Bringloe	–	–	<a href="#">MN184245</a>
<i>Ceramium pallidum pallidum</i>	–	2016_ BIO309A_47	Norway: Hordaland, Sore egdholmen	18.04.2016	C.M. Berntsen, N.E. Frogg & C.C. Martin	–	–	<a href="#">MN184273</a>
<i>Ceramium rothianum</i> M.A.Wolf, K.Sciuto, I. Moro, Maggs & Sfriso	–	–	Italy: Ca' Roman, Pellestrina	–	–	<a href="#">LR031258</a>	–	–
<i>Ceramium secundatum</i> Lyngbye	–	CAM 41	Ireland: St John's Pt, Co. Donegal	20.II.1992	CAM	<a href="#">AF439287</a>	–	–
<i>Ceramium secundatum</i>	–	CAM 355	Dale Fort, Pems, Wales	10.X.1995	CAM	<a href="#">AF439286</a>	–	–
<i>Ceramium secundatum</i>	–	–	France: Bretagne, Roscoff	5.IV.2000	Yang E.C. & Boo S.M.	–	–	<a href="#">EU194972</a>
<i>Ceramium secundatum</i>	–	IN07.R036	UK:Tristan da Cunha, Saint Helena, Inaccessible, Off Tom's Beach	29.XI.2007	Susan Scott	<a href="#">MK185826</a>	–	–

APPENDIX 2. — Continuation.

Sample	Herbaria/ GenBank names	Sample number	Location and specimen voucher	Date collected	Collector	GenBank accession number		
						<i>rbcL</i>	Partial LSU	COI-5P
<i>Ceramium secundatum</i>	–	Tristan 2010 073	Saint Helena: Tristan, West of Harbour, pools	31.III.2010	Susan Scott	–	–	<a href="#">MK202399</a>
<i>Ceramium secundatum</i>	–	Nightingale 2010 056	Saint Helena: Nightingale, East Landing	23.III.2010	Susan Scott	–	–	<a href="#">MK202407</a>
<i>Ceramium secundatum</i>	–	GWS018041	US: Fort Witherill, Jamestown, Rhode Island	16.IV.2016	B. Clarkston, D. McDevit, M. Bruce, A. Savoie & C. Longtin	<a href="#">KT250273</a>	–	<a href="#">KT250208</a>
<i>Ceramium secundatum</i>	–	2016_ BIO309A_30	Norway: Hordaland, Espesgrend	17.IV.2016	C.S. Armitage	–	–	<a href="#">MN184367</a>
<i>Ceramium secundatum</i>	–	GWS038089	Norway: Station Dorm Beach, Espesgrend	3.VI.2016	G.W. Saunders & T. Bringle	–	–	<a href="#">MN184499</a>
<i>Ceramium shuttleworthianum</i> (Kützing) Rabenhorst	–	CAM 1049	UK: Broad Haven Beach, Wales	17.III.2003	CAM	<a href="#">FR871404</a>	–	–
<i>Ceramium shuttleworthianum</i>	–	GWS039860	Norway: Hellesoy	5.VI.2016	G.W. Saunders & T. Bringle	<a href="#">MN184563</a>	–	<a href="#">MN184486</a>
<i>Ceramium siliquosum</i> (Kützing) Maggs & Hommersand	–	CAM 172	Ireland: Fanore, Co. Clare	28.IX.1992	CAM	<a href="#">FR871405</a>	–	–
<i>Ceramium siliquosum</i>	–	RMAR1120	France: Brittany, Les Rospects	14.III.2011	Le Gall L. & Turpin Y.	–	–	<a href="#">KJ960523</a>
<i>Ceramium strictum</i> Roth	–	CAM 140	Ireland: Skerries, Co. Dublin	30.VIII.1992	CAM	<a href="#">FR871408</a>	–	–
<i>Ceramium tenuicorne</i> (Kützing) Waern	–	Rueness 9817	Culture	4.X.1994	B. Eklund	<a href="#">FR871409</a>	–	–
<i>Ceramium virgatum</i> Roth	–	CAM 496	Germany: South Harbour, Helgoland, North Sea	7.I.1999	A. Wagner	<a href="#">AF439290</a>	–	–
<i>Ceramium virgatum</i>	–	GWS003615	USA: Maine, Cape Neddick, southern ME	24.IV.2006	L. Le Gall	–	–	<a href="#">KT250188</a>
<i>Ceramium virgatum</i>	–	GWS014784	USA: Massachusetts, Folly Cove, Gloucester, right side	13.IV.2010	B. Clarkston & A. Savoie	<a href="#">KT250272</a>	–	<a href="#">KT250206</a>
<i>Ceramium virgatum</i>	–	GWS002366 or GWS2366	Canada: Nova Scotia, Cape St. Marys	5.IX.2004	G.W. Saunders	–	<a href="#">EF033604</a>	<a href="#">KT250235</a>
<i>Ceramium</i> sp. 1	<i>Ceramium</i> sp.	2016_ BIO309A_66	Norway: Hordaland, Stora Kalsoy	19.IV.2016	T. Ulvatn & H. Dybevik	<a href="#">MN184543</a>	–	<a href="#">MN184330</a>
<i>Ceramium</i> sp. 2	<i>Ceramium secundatum</i>	LM 1565	New Zealand: Christchurch; culture	I.2003	M.P. Johnson	<a href="#">MW366509</a>	<a href="#">MW354749</a>	<a href="#">MW354763</a>
<i>Ceramium</i> sp. 3	<i>Ceramium</i> sp. 1	GWS040811	Norway: Hakonsund	10.VI.2016	G.W. Saunders & T. Bringle	<a href="#">MN184529</a>	–	<a href="#">MN184247</a>
<i>Ceramium</i> sp. 4	–	LM 1562	Tenerife, Spain	2003	LM	<a href="#">MW366507</a>	–	–
<i>Ceramium</i> sp. 5	–	CAM 1130	Italy: Ischia; culture	7.XII.2002	CAM	<a href="#">FR871407</a>	–	–
<i>Corallophila atlantica</i> (A.B.Joly & Ugadim) R.E.Norris	–	MBBB 146	Brazil: Prainha, Arraial do Cabo, Rio de Janeiro. RB420071	27.VII.2005	MBBB	<a href="#">MW366512</a>	–	<a href="#">MW354761</a>

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Sample	Herbaria/ GenBank names	Sample number	Location and specimen voucher	Date collected	Collector	GenBank accession number		
						<i>rbcL</i>	Partial LSU	COI-5P
<i>Corallophila atlantica</i>	–	MBBB 457	Brazil: Praia da Tartaruga, Armação de Búzios, Rio de Janeiro	11.IX.2015	MBBB	–	–	MW354774
<i>Corallophila atlantica</i>	–	MBBB 458	Brazil: Praia da Tartaruga, Armação de Búzios, Rio de Janeiro	11.IX.2015	MBBB	MW366536	–	MW354775
<i>Corallophila eatoniana</i> (Farlow) T.O.Cho, H.-G.Choi, G.I.Hansen & S.M.Boo	<i>Ceramium eatonianum</i> (Farlow) De Toni	GWS021384	USA: California, Pigeon Point Lighthouse	15.V.2010	B. Clarkston & K. Hind	–	–	KM254535
<i>Corallophila eatoniana</i>	–	XX1109	USA: California	–	E. Serrão	DQ458957	–	–
<i>Corallophila eatoniana</i>	–	TC047	USA: Friday harbor, Washington	16.VII.1998	T.O. Cho	AY945765	DQ238802	–
<i>Corallophila eatoniana</i>	–	AC135	Canada: B.C., Vancouver Is.	5.VII.2004	AC	GQ252469	–	–
<i>Corallophila eatoniana</i>	–	–	USA: Oregon, Crystal Core	15.XII.1999	–	DQ787568	–	–
<i>Corallophila eatoniana</i>	<i>Ceramium eatonianum</i>	GWS021391	USA: California, Santa Cruz (Four Mile)	15.V.2010	B. Clarkston & K. Hind	–	–	HQ544058
<i>Corallophila eatoniana</i>	<i>Ceramium eatonianum</i>	GWS021384	USA: California, Pigeon Point Lighthouse	15.V.2010	B. Clarkston & K. Hind	–	–	KM254535
<i>Corallophila huysmansii</i> (Weber-van Bosse) R.E.Norris	–	ARS03236	USA: Hawaii, Kure Atoll	30.XI.1999	Abbott collection	–	HQ421935	HQ422782
<i>Corallophila</i> sp.	<i>Ceramium</i> sp.	ARS03774	USA: Hawaii	–	–	–	HQ422146	–
<i>Gayliella ardissoni</i> Barros-Barreto & F.P.Gomes	<i>Ceramium flaccidum</i>	MBBB 26	Brazil: Ponta da Baleia, Aracruz, Espírito Santo. RB420056	7.VII.2002	MBBB	DQ458944	–	–
<i>Gayliella ardissoni</i>	<i>Ceramium flaccidum</i>	MBBB 50	Brazil: Praia Mole, Vitória, Espírito Santo. RB420057	1.VIII.2003	MBBB	–	–	MN105046
<i>Gayliella ardissoni</i>	<i>Ceramium flaccidum</i>	MBBB 51	Brazil: Praia Mole, Vitória, Espírito Santo. RB420058	1.VIII.2003	MBBB	DQ458946	MN105050	MN105047
<i>Gayliella dawsonii</i> (A.B.Joly) Barros-Barreto & F.P.Gomes	<i>Ceramium dawsonii</i>	MBBB 53	Brazil: Redonda Sul, Abrolhos, Bahia. RB420047	14.XII.2002	MBBB	DQ458938	–	MN105032
<i>Gayliella dawsonii</i>	–	FPG234	Praia do Gonzaguinha, São Vicente, São Paulo. Brazil. R232583	12.10.2016	F.P. Gomes	–	MN105057	–
<i>Gayliella fimbriata</i> (Setchell & N.L.Gardner) T.O.Cho & S.M.Boo	–	AC202	USA: HI, Maui	8.IV.2006	–	GQ252474	–	–
<i>Gayliella flaccida</i> (Harvey ex Kützing) T.O.Cho & L.J.Mclvor	–	CAM 113	UK: Beau Port, Jersey, Channel Islands	12.VIII.1992	CAM	AY945778	–	–
<i>Gayliella iemanja</i> Barros-Barreto & F.P.Gomes	<i>Ceramium dawsonii</i>	MBBB 34	Brazil: Serrambi, Pernambuco. RB420045	14.XII.2001	J. Torres & L. Gestinari	DQ458936	MN105052	MN105039
<i>Gayliella jolyana</i> Barros-Barreto & F.P.Gomes	<i>Ceramium dawsonii</i>	MBBB 49	Brazil: Peracanga, Guarapari, Espírito Santo. RB420046	31.VII.2003	MBBB	DQ458937	MN105061	MN105033



APPENDIX 2. — Continuation.

Sample	Herbaria/ GenBank names	Sample number	Location and specimen voucher	Date collected	Collector	GenBank accession number		
						<i>rbcL</i>	Partial LSU	COI-5P
<i>Gayliella jolyana</i>	<i>Ceramium dawsonii</i>	MBBB 69	Brazil: Prainha, Arraial do Cabo, Rio de Janeiro. RB420050	29.VII.2001	MBBB	–	MN105060	MN105036
<i>Gayliella mazoyerae</i> T.O.Cho, Fredericq & Hommersand	–	–	Italy: Sicily	XII.2003	Cormaci	AY945776	DQ238809	–
<i>Gayliella nanaoensis</i>	<i>Gayliella</i> sp.	HTa-2020a	China	–	Tan Huaqiang	MN592682	–	–
<i>Gayliella tamoiensis</i> Barros-Barreto & F.P.Gomes	–	MBB 241	Brazil: Praia Rasa, Armacao dos Buzios, RJ. R232576	2.VI.2011	MBBB	MN105075	MN105055	MN105028
<i>Gayliella tamoiensis</i>	–	MBB 434	Brazil: Praia Rasa, Armacao dos Buzios, RJ. R232578	2.VI.2011	MBBB	–	MN105056	MN105025
<i>Gayliella taylorii</i> (E.Y.Dawson) T.O.Cho & S.M.Boo	–	TC255	USA: Crystal Cove, Orange Co., California	3.VII.1999	T.O. Cho & S.N. Murray	AY945774	–	–
<i>Gayliella taylorii</i>	–	–	USA: Laguna Beach, Orange Co., California	3.XII.1999	T.O. Cho & S.N. Murray	–	DQ238812	–
<i>Gayliella transversalis</i> (Collins & Hervey) T.O.Cho & Fredericq	<i>Gayliella keywestiensis</i>	TC961	USA: Key West, Florida	30.XI.2003	T.O. Cho	AY945777	DQ238810	–
<i>Gayliella womersleyi</i> T.O.Cho, Maggs & L.Mclvor	<i>Gayliella miniatum</i>	C1507	Australia: Williamstown	13.III.2002	M.D. Guiry	AY945780	DQ238808	–
<i>Gayliella</i> sp. 1	<i>Gayliella</i> sp.	AC165	Mexico: Baja CA, Cabo San Quintin	20.III.2005		GQ252475		
<i>Gayliella</i> sp. 2	–	JAW 4461	Australia: Williamstown; culture	24.VII.2004	J.A. West	MW366510	–	–
<i>Gayliella</i> sp. 3	<i>Gayliella</i> sp. 1 JFC-2019	HV06133	Australia: VIC, Mallacoota		Heroen Verbruggen & Kyatt Dixon	MK125376	–	–
<i>Gayliella</i> sp. 4	–	FPG 202	Brazil: Praia do Gonzaguinha, Sao Vicente, SP. R232573	12.X.2016	F.P. Gomes	MN105065	MN105054	MN105038
<i>Gayliella</i> sp. 5	–	FPG 125	Brazil: Praia da Pedra Rachada, Paracuru, CE. R232568	4.VI.2016	F.P. Gomes	–	MN105051	MN105042
<i>Gayliella</i> sp. 6	–	ARS03583	USA: Hawaii, Molokai, Wavecrest	21.III.2008	K. Conklin	–	HQ422107	HQ422894
<i>Gayliella</i> sp. 7	–	ARS03693	USA: Hawaii, Lanai	28.III.2008	A. Kurihara	–	HQ422193	HQ422977
<i>Gayliella</i> sp. 8	–	ARS03689	USA: Hawaii, Oahu, Nanakuli	12.III.2008	A. Kurihara	–	HQ422171	HQ422973
<i>Gayliella</i> sp. 9	–	ARS03846	USA: Hawaii, Oahu, Makai Pier	08.VI.2008	A. Kurihara	–	HQ422195	HQ423004
<i>Herpochondria borealis</i> (Ruprecht) Barros-Barreto & Maggs, comb. nov.	<i>Microcladia borealis</i> Ruprecht	CAM 424	USA: Salt Creek, Crescent Bay, Washington. NCU-A-0020296	09.VI.1994	MHH	MW366515	–	–
<i>Herpochondria borealis</i>	<i>Microcladia borealis</i>	TC391	USA: Lone Ranch Beach, Brookings, Josephine Co., Oregon	18.V.1999	MHH	EF613514	–	–
<i>Herpochondria borealis</i>	<i>Microcladia borealis</i>	–	USA: Otter Crest, Oregon	12.VII.1998	T.O. Cho & G.I. Hansen	–	DQ238799	–

## APPENDIX 2. — Continuation.

Sample	Herbaria/ GenBank names	Sample number	Location and specimen voucher	Date collected	Collector	GenBank accession number		
						<i>rbcL</i>	Partial LSU	COI-5P
<i>Herpochondria corallinae</i> (G.Martens) Falkenberg	–	H6	South Korea: Jeongdori, Wando	10.VII.1998	S.M. Boo, T.O. Cho & H.G. Choi	DQ787569	–	–
<i>Herpochondria elegans</i> (Okamura) Itono	–	TC037	South Korea: Jeongdori, Wando	15.XII.1998	S.M. Boo, T.O. Cho & H.G. Choi	AY945771	DQ238800	–
<i>Pseudoceramium brevizonatum</i> (H.E.Petersen) Barros-Barreto & Maggs, comb. nov	–	CAM 240	Italy: Pietro Ligure, Liguria. BM000701867	19.VII.1993	CAM	MW366524	–	–
<i>Pseudoceramium caraibicum</i> (H.E.Petersen & Borgesen) Barros- Barreto, Maggs & M.A.Jaramillo, comb. nov., stat. nov.	<i>Ceramium brevizonatum</i> H.E.Petersen	–	Mexico: Yucatan	13.II.1993	C.F.D. Gurgel	AF259491	–	–
<i>Pseudoceramium clarionense</i> (Setchell & N.L. Gardner) Barros- Barreto & Maggs, comb. nov.	<i>Ceramium clarionense</i> Setchell & N.L.Gardner	MBBB 76	Brazil: Siriba, Abrolhos, Bahia. RB420036	13.XII.2002	MBBB	DQ458933	–	–
<i>Pseudoceramium inkyui</i> (T.O.Cho, Fredericq & S.M.Boo) Barros- Barreto & Maggs, comb. nov.	<i>Ceramium inkyui</i> T.O.Cho, Fredericq & S.M.Boo	–	South Korea: Sinnam, Kangwon	7.VII.1999	T.O. Cho	MW366527	–	–
<i>Pseudoceramium paniculatum</i> (Okamura) Barros-Barreto & Maggs, comb. nov.	<i>Ceramium paniculatum</i> Okamura	–	South Korea: Gampo, Kyungbuk	8.IX.1999	S.M. Boo & T.C. Cho	AF521802	–	–
<i>Pseudoceramium planum</i> (Kützing) Barros-Barreto & Maggs, comb. nov.	<i>Ceramium planum</i> Kützing	CAM 413	South Africa: Kommetjie, Western Cape	9.XI.1999	MHH	MW366527	–	–
<i>Pseudoceramium oliveirarum</i> Barros- Barreto, Maggs & M.A.Jaramillo, gen. nov., sp. nov.	<i>Ceramium brevizonatum</i> var. <i>caraibicum</i> H.E.Petersen & Borgesen	MBBB 47	Brazil: Costão, Itapemirim, Espírito Santo. RB420029	4.III.2004	MBBB	–	MW354756	–
<i>Pseudoceramium oliveirarum</i>	<i>Ceramium brevizonatum</i> var. <i>caraibicum</i>	MBBB 98	Brazil: Ponta do Páí Vitória, Armação dos Búzios, Rio de Janeiro. RB420031	10.VII.2005	MBBB	–	–	MW354770
<i>Pseudoceramium oliveirarum</i>	<i>Ceramium brevizonatum</i> var. <i>caraibicum</i>	MBBB 80	Brazil: Guaibura, Guarapari, Espírito Santo. RB420030	31.VII.2003	MBBB	DQ458932	–	–
<i>Pseudoceramium tenerrimum</i> (G.Martens) Barros-Barreto & Maggs, comb. nov.	<i>Ceramium tenerrimum</i>	–	South Korea: Namhae, Kyungnam	30.V.1999	T.O. Cho & H.S. Yoon	AF521805	–	–
<i>Pseudoceramium tenerrimum</i>	<i>Ceramium tenerrimum</i>	AC209	South Korea: Jeju City, Yongdam	11.V.2006	–	GQ252467	–	–
<i>Pseudoceramium tenerrimum</i>	<i>Ceramium tenerrimum</i>	–	South Korea: Gampo, Kyengju	8.IX.1999	T.O. Cho	–	DQ238805	–
<i>Pseudoceramium tenerrimum</i>	<i>Ceramium tenerrimum</i>	LQDHQW2012	China: Huiquan Bay, Qingdao	12.V.2012	Wu F.-F.	–	KC795867	–
<i>Pseudoceramium</i> sp. 1	–	CAM 1654	Marigot, St Martin, Dutch Antilles. BM013821502	19.I.2005	W. Prud'homme van Reine	MW366523	–	–
<i>Pseudoceramium</i> sp. 2	<i>Ceramium tenerrimum</i>	MBBB 77	Redonda Sul, Abrolhos, BA; Brazil. RB420068	14.XII.2002	MBBB	DQ458954	–	–
<i>Reiboldiella filicula</i> (Harvey ex Womersley) Barros-Barreto & Maggs, comb. nov.	<i>Ceramium filicula</i> Harvey ex Womersley	XX1015	Australia: Melbourne, Williamstown	–	J.C. Zuccarello	DQ458956	–	–
<i>Reiboldiella filicula</i>	<i>Ceramium filicula</i>	MBBB 17	Brazil: Praia Vermelha, Urca, Rio de Janeiro. RB420054	13.IX.2004	W. Paradas	DQ458942	–	MW354768

APPENDIX 2. — Continuation.

Sample	Herbaria/ GenBank names	Sample number	Location and specimen voucher	Date collected	Collector	GenBank accession number		
						<i>rbcL</i>	Partial LSU	COI-5P
<i>Reinboldiella orientalis</i> S.-M.Lin & Mas.Suzuki	–	RO-CJ3	Taiwan: Keelung, Chaojing	5.V.2016	S.-M. Lin	LC201458	–	–
<i>Reinboldiella orientalis</i>	–	RO-CJ4	Taiwan: Keelung, Chaojing	5.V.2016	S.-M. Lin	LC201459	–	–
<i>Reinboldiella schmitziana</i> (Reinbold) De Toni	–	TC032	South Korea: Guryongpo, Pohang	4.V.1998	T.O. Cho & H.S. Yoon	AY945772	–	–
<i>Reinboldiella schmitziana</i>	–	RS-JP	South Korea: Guryongpo, Pohang	5.VI.2009	S.-M. Lin & M. Suzuki	LC201465	–	–
<i>Reinboldiella taiwanensis</i> S.-M.Lin & Mas.Suzuki	–	RT-CJ1	Taiwan: Chaojing, Keelung	7.04.2016	S.-M. Lin	LC201467	–	–
<i>Reinboldiella taiwanensis</i>	–	RT-CJ2	Taiwan: Chaojing, Keelung	7.04.2016	S.-M. Lin	LC201468	–	–
<i>Reinboldiella warburgii</i> (Heydrich) Yoshida & Mikami	–	–	Taiwan: St. Tiago, Taipei Co.	22.V.2005	S.-M. Lin	EF125878	–	–
<i>Reinboldiella warburgii</i>	–	RW-CJ	Taiwan: Chaojing, Keelung	28.IV.2009	M. Suzuki	LC201471	–	–
<i>Stirkia brasiliensis</i> (A.B.Joly) Barros-Barreto & Maggs, comb. nov.	<i>Ceramium brasiliense</i> A.B.Joly	MBBB 41	Brazil: Boa Viagem, Recife, Pernambuco. RB420020	15.XII.2001	J. Torres & L. Gestinari	DQ458922	MW354747	MW354760
<i>Stirkia codii</i> (J.Agardh) Barros-Barreto & Maggs, comb. nov.	<i>Ceramium codii</i> J.Agardh	–	USA: Hawaii, Kure Atoll	8.VII.1998	T.O. Cho & G.I. Hansen	–	HQ421967	–
<i>Stirkia codicola</i> (J.Agardh) Barros-Barreto & Maggs, comb. nov.	<i>Ceramium codicola</i> J.Agardh	–	USA: Boiler Bay, Oregon	8.VII.1998	T.O. Cho & G.I. Hansen	AY155522	DQ238806	–
<i>Stirkia coulteri</i> (Harvey) Barros-Barreto & Maggs, comb. nov.	<i>Microcladia coulteri</i> Harvey	CAM 402	USA: Asilomar Beach, California. BM013821501	17.VII.1996	CAM	MW366528	–	–
<i>Stirkia coulteri</i>	<i>Microcladia coulteri</i>	AC263	USA: WA, San Juan Is.	18.VIII.2006	Carlile A. L.	GQ252482	–	–
<i>Stirkia coulteri</i>	<i>Microcladia coulteri</i>	GWS022133	USA: California, Stillwater Cove, Pebble Beach	20.V.2010	B. Clarkston, K. Hind & S. Toews	–	–	KM254414
<i>Stirkia dumoserta</i> (R.E.Norris & I.A.Abbott) Barros-Barreto & Maggs, comb. nov.	<i>Ceramium dumosertum</i> R.E.Norris & I.A.Abbott	AC191	USA: Hawaii, Kihei, Maui	5.IV.2006	Carlile A. L.	GQ252454	–	–
<i>Stirkia dumoserta</i>	<i>Cer. dumosertum</i>	ARS00847	USA: Hawaii, Maui, Lipoa St	5.IV.2006	Carlile A. L.	–	HQ421685	HQ422603
<i>Stirkia fujiana</i> (Barros-Barreto & Maggs) Barros-Barreto & Maggs, comb. nov.	<i>Ceramium fujianum</i> Barros-Barreto & Maggs	MBBB 22	Brazil: Itacuruça, Cananéia, Sao Paulo. RB420061	16.VI.2003	M.T. Fujii	DQ458949	MW354750	MW354758
<i>Stirkia fujiana</i>	<i>Ceramium fujianum</i>	MBBB 82	Brazil: Praia Baleia, Manguinhos, Espirito Santo. RB420063	26.III.2005	M.T. Fujii	–	–	MW354759
<i>Stirkia fujiana</i>	<i>Ceramium fujianum</i>	MBBB 84	Brazil: Portal de Santa Cruz, Espirito Santo. RB420064	25.III.2005	M.T. Fujii	DQ458952	–	–
<i>Stirkia horrida</i> (Setchell & N.L.Gardner) Barros-Barreto & Maggs, comb. nov.	<i>Ceramium horridum</i> Setchell & N.L.Gardner	–	México: San Juan de la Costa, Baja California	15.VI.2000	T.O. Cho & R.R.-Rodriguez	AF521796	DQ238807	–
<i>Stirkia incospicua</i> (Zanardini) Barros-Barreto & Maggs, comb. nov.	<i>Ceramium incospicuum</i> Zanardini	–	Alberoni dyke, Lido of Venice	–	–	LR031255	–	–



## APPENDIX 2. — Continuation.

Sample	Herbaria/ GenBank names	Sample number	Location and specimen voucher	Date collected	Collector	GenBank accession number		
						<i>rbcL</i>	Partial LSU	COI-5P
<i>Stirkia interrupta</i> (Setchell & Gardner) Barros-Barreto & Maggs, comb. nov.	<i>Ceramium interruptum</i> Setchell & Gardner	–	USA: Dana Point, California	4.XII.1999	T.O. Cho & S. Murray	AY155527	–	–
<i>Stirkia japonica</i> (Okamura) Barros-Barreto & Maggs, comb. nov.	<i>Ceramium japonicum</i> Okamura	–	South Korea: Namhae, Kyengnam	3.III.1998	T.O. Cho	AY948753	–	–
<i>Stirkia japonica</i>	<i>Ceramium japonicum</i>	LQDHQW2012 1115-R5	China: Huiquan Bay, Qingdao	11.XI.2012	Wu F.-F.	–	KC795870	–
<i>Stirkia japonica</i>	<i>Ceramium japonicum</i>	CQDHQW2012 1115-R5	China: Huiquan Bay, Qingdao	21.XI.2012	Wu F.-F.	–	–	KC795912
<i>Stirkia juliae</i> (A.J.K.Millar) Barros-Barreto & Maggs, comb. nov.	<i>Ceramium juliae</i> A.J.K.Millar	–	South Africa: culture		W. Stirk	MW366506	–	–
<i>Stirkia pacifica</i> (Collins) Barros-Barreto & Maggs, comb. nov.	<i>Ceramium pacificum</i> (Collins) Kylin	AC306	USA: Washington, San Juan Island	29.VII.2007	Carlile A. L.	FJ795539	–	–
<i>Stirkia pacifica</i>	<i>Ceramium pacificum</i>	AC286	USA: WA, Clallam Co., Cape Alava	18.VI.2007	Carlile A. L.	GQ179817	–	–
<i>Stirkia riosmenae</i> (B.Y.Won & T.O.Cho) Barros-Barreto & Maggs, comb. nov.	<i>Ceramium riosmenae</i> B.Y.Won & T.O.Cho	TC245	Mexico: B.C.S., Bahía Magdalena, López Nateos, Estero Santo Domingo	1.VI.2000	T.O. Cho & R.R.-Rodríguez	JN712693	–	–
<i>Stirkia sinicola</i> (Setchell & Gardner) Barros-Barreto & Maggs, comb. nov.	<i>Ceramium sinicola</i> Setchell & Gardner	DANA	USA: Dana Point, California	4.XII.1999	T.O. Cho & S. Murray	AY155531	–	–
<i>Stirkia sinicola</i>	<i>Ceramium sinicola</i>	AC298	USA: CA, Santa Cruz Co., Greyhound Rock	3.VII.2007	–	GQ179818	–	–
<i>Stirkia vaga</i> (P.C.Silva) Barros-Barreto & Maggs, comb. nov.	<i>Ceramium vagans</i> P.C.Silva	MBBB 126	Brazil: Praia da Feiticeira, Ilha Grande, Mangaratiba, Rio de Janeiro. RB420069	29.VII.2005	MBBB	MW366529	–	MW354772
<i>Stirkia</i> sp. 1	–	CAM 1144	Chile: Caldera. BM013821505	–	Juan Correa	MW366508	–	–
<i>Stirkia</i> sp. 2	–	MBBB 110	Brazil: Prainha, Arraial do Cabo, Rio de Janeiro. RB420052	27.VII.2005	MBBB	MW366530	–	MW354771
<i>Stirkia</i> sp. 3	<i>Ceramium</i> sp. 2	DWF-2013	USA: North Carolina, Onslow Bay, Atlantic Ocean, Wynne Plaza Park. NCweed1227	18.II.2013	Freshwater	KF367768	–	–
<i>Stirkia</i> sp. 4	<i>Ceramium</i> sp.	ARS01431	USA: Hawaii	–	–	–	HQ422441	–
<i>Stirkia</i> sp. 5	<i>Ceramium</i> sp.	ARS03593	USA: Hawaii	–	–	–	HQ422096	–
<i>Yoneshiguea affinis</i> (Setchell & N.L.Gardner) Barros-Barreto, Maggs & M.A.Jaramillo, comb. nov.	<i>Ceramium affine</i> Setchell & N.L.Gardner	–	México: Pichilingue, Baja California	27.V.2000	T.O. Cho & R.R.-Rodríguez	AF521797	DQ238803	–
<i>Yoneshiguea affinis</i>	<i>Ceramium affine</i>	MBBB 65	Brazil: Lagoinha, Ubatuba, Sao Paulo. RB420018	24.V.2003	M.T. Fujii	DQ458920	MW354755	MW354769
<i>Yoneshiguea compta</i> (Børgesen) Barros-Barreto, Maggs & M.A.Jaramillo, comb. nov.	<i>Ceramium comptum</i> Børgesen	MBBB 118	Brazil: Lagoa Azul, Ilha Grande, Mangaratiba, Rio de Janeiro. RB420041	29.VII.05	MBBB	MW366522	–	–
<i>Yoneshiguea</i> sp.	–	JAW 3507	French Polynesia: Cooks Bay, Moorea; culture	1.VII.1995	J.A. West	MW366521	–	–

APPENDIX 2. — Continuation.

Sample	Herbaria/ GenBank names	Sample number	Location and specimen voucher	Date collected	Collector	GenBank accession number		
						<i>rbcL</i>	Partial LSU	COI-5P
Ceramieae sp. 1	–	CAM 1133	France: Thau Lagoon	VI.2005	M. Verlaque	MW366525		
Ceramieae sp. 2	<i>Microcladia alternata</i>	Nightingale 2010 040	UK: Tristan da Cunha, Saint Helena: Nightingale, Southwest Point	22.III.2010	Susan Scott	MK185813	–	MK202416
Ceramieae sp. 3	<i>Ceramium tenuissimum</i> (Roth) J.Agardh	AC213	South Korea: Jeju Is., Onpyong	12.V.2006	–	GQ252468	–	–
Ceramieae sp. 4	–	MBBB 156	Brazil: Laje de Santos, São Paulo. RB420038	5.XI.2005	MBBB	MW366513	–	MW354766
Ceramieae sp. 4	–	MBBB 157	Brazil: Laje de Santos, São Paulo. RB420039	5.XI.2005	MBBB	–	–	MW354767
Ceramieae sp. 5	<i>Ceramium nitens</i> (C.Agardh) J.Agardh	MBBB 83	Brazil: Pontal de Maracaípe, Ipojuca, Pernambuco. RB420066	28.I.2005	M.T. Fujii	DQ458953	MW354754	MW354762
Ceramieae sp. 6	–	JAW 4446	Madagascar: Airport Lagoon, I. St. Marie. BM000701862	22.V.2004	J.A. West	MW366511	–	–
Ceramieae sp. 7	<i>Ceramium womersleyi</i> R.E.Norris & I.A.Abbott	ARS01943	USA: Hawaii, Maui, Lipoa St	28.I.2007	T. Sauvage	–	HQ422536	HQ423060
Ceramieae sp. 8	<i>Ceramium hanaense</i> R.E.Norris & I.A.Abbott	ARS03261	USA: Hawaii, Kure Atoll	30.XI.1999	Abbott collection	–	HQ421934	HQ422844
Ceramieae sp. 9	<i>Campylaeophora californica</i> (Farlow) T.O.Cho	GWS021269	USA: California, Pigeon Point Lighthouse	15.V.2010	B. Clarkston & K. Hind	–	–	KM254681
Ceramieae sp. 10	<i>Ceramium diaphanum</i> (Lightfoot) Roth	CQDSLR2011 1028-R8	China	12.X.2011	Wu F.-F	–	–	KC795911
Ceramieae sp. 11	<i>Microcladia</i> sp.	GWS021844	USA: California, Jade Cove	18.V.2010	B. Clarkston & K. Hind	–	–	KM254932
Ceramieae sp. 12	<i>Ceramium diaphanum</i>	LQDSLR2011 1028-R8	China	12.X.2011	Wu F.-F	–	KC795860	–
Ceramieae sp. 13	<i>Ceramium</i> sp.	ARS03540	USA: Hawaii	–	–	–	HQ422054	–
Ceramieae sp. 14	<i>Ceramium</i> sp.	ARS00852	USA: Hawaii	–	–	–	HQ421687	–
Ceramieae sp. 15	<i>Ceramium</i> sp.	ARS03153	USA: Hawaii	–	–	–	HQ422004	–
Ceramieae sp. 16	<i>Ceramium</i> sp.	ARS03197	USA: Hawaii	–	–	–	HQ422033	–
Ceramieae sp. 17	<i>Ceramium</i> sp.	ARS03032	USA: Hawaii	–	–	–	HQ421931	–
Ceramieae sp. 18	<i>Ceramium</i> sp.	ARS03848	USA: Hawaii	–	–	–	HQ422196	–
Ceramieae sp. 19	<i>Ceramium</i> sp.	ARS03260	USA: Hawaii	–	–	–	HQ421961	–
Ceramieae sp. 20	<i>Ceramium</i> sp.	ARS03687	USA: Hawaii	–	–	–	HQ422173	–
Ceramieae sp. 21	<i>Ceramium</i> sp.	ARS03571	USA: Hawaii	–	–	–	HQ422110	–
<b>Outgroup</b>								
<i>Aglaothamnion uruguayense</i> (W.R.Taylor) N.E.Aponte, D.L.Ballantine & J.N.Norris	–	MBBB 147	Brazil: Praia Rasa, Búzios, Rio de Janeiro. RB631393	9.VII.2005	MBBB	–	–	MW354773

## APPENDIX 2. — Continuation.

Sample	Herbaria/ GenBank names	Sample number	Location and specimen voucher	Date collected	Collector	GenBank accession number		
						<i>rbcL</i>	Partial LSU	COI-5P
<i>Aglaothamnion tenuissimum</i> (Bonnemaison) Feldmann-Mazoyer	–	CAM 114	Spain: Cudillero Harbor, Asturias; culture. BM000701860	6.III.1999	CAM	<a href="#">MW366516</a>	–	–
<i>Antithamnion nipponicum</i> Yamada & Inagaki	–	1078 Kobe University	Japan: Hachinohe, Aomori		M. Kamiya	–	<a href="#">DQ238813</a>	–
<i>Ptilota serrata</i> Kylin	–	GWS002173	Canada: British Columbia	16.VI.2000	–	–	–	<a href="#">AY970640</a>
<i>Seirospora interrupta</i> (Smith) F.Schmitz	–	Clone N484	UK: Sarn Badrig, Cardigan Bay, Caernavon, Wales	15.VIII.1998	CAM	<a href="#">AF439310</a>	–	–
<i>Spermothamnion repens</i> (Dillwyn) Magnus	–	CBS IUCC1412, MA, USA	USA: Massachusetts	–	–	<a href="#">U04024</a>	–	–
<i>Sphondylothamnion multifidum</i> (Hudson) Nägeli	–	Clone N471	UK: Sarn Badrig, Cardigan Bay, Caernavon, Wales	20.VIII.1998	CAM	<a href="#">AF439312</a>	–	–
<i>Spyridia filamentosa</i> (Wulfen) Harvey	–	PR2946	Puerto Rico: Cayo Enrique; culture	16.III.1989	–	<a href="#">AF458705</a>	–	–

APPENDIX 3. — Data matrix with morphological characters. Symbols: –, missing or non available data; ?, unknown data; \*, data from this study.

Taxon/Characters	1	2	3	4	5	6	7	8	9	10	11	12	References
<i>Aglaothamnion tenuissimum</i>	0	4	0	2	0	0	1	2	1	0	0	0	*
<i>Campylaephora borealis</i> AY945767	0	1	?	1	?	1	?	0	2	?	2	4	7, 21
<i>Campylaephora boydenii</i> 412	0	1	3	1	2	1	?	0	0, 1	0	2	4	*, 21
<i>Campylaephora californica</i> EF613500	0	1	3	1	2	1	0	0	2	2	2	4	8, 13, 21
<i>Campylaephora californica</i> 2 MW366519	1	1	3	1	2	1	0	0	1	2	2	4	*
<i>Campylaephora crassa</i> AY945769	0	1	?	1	2	1	0	–	–	–	–	4	7, 21
<i>Campylaephora hypnaeoides</i> JA EF613505	0	1	?	1	?	1	0	–	–	–	–	4	7, 21
<i>Campylaephora hypnaeoides</i> KO EF613506	0	1	–	1	–	1	0	–	–	?	2	4	7, 21
<i>Campylaephora kondoi</i> AY295176	0	1	0	1	2	0	0	0	2	2	2	4	3, 9
<i>Carpoblepharis flaccida</i> AY945764	1	1	2	1	?	0	1	0	2	2	3	2	6, 13
<i>Carpoblepharis obsoleta</i> FR871402	0	1	?	1	?	?	?	?	1	1	0	2	*, 23
<i>Carpoblepharis</i> sp. FR871406	0	1	2	1	2	0	0	1	2	2	2	4	*
<i>Ceलेceras monile</i>	0	1	0, 1	0	1, 2	0	0	0	0, 1	1	0, 2	5	*, 27
<i>Ceलेceras nova-zealandiae</i> 411	1	1	3	1	3	0	0	?	?	?	?	5	*, 13
<i>Ceलेceras pusilla</i> FR871403	0	1, 2	2	0, 1	2	0	0	0	2	1	2	5	*, 27
<i>Centroceras arcii</i> KP222800	0	4	1	1	0	0	0	0	?	0	?	0	20
<i>Centroceras clavulatum</i> PE DQ374331	0	3	1	1	1	0	0	0	2	2	0	5	30
<i>Centroceras gasparrinii</i> AU DQ374321	0	1	–	–	–	–	–	?	?	1	?	5	30
<i>Centroceras gasparrinii</i> BE KP222805	0	4	1	1	1	0	0	–	–	–	–	0	20
<i>Centroceras gasparrinii</i> BR1 DQ374311	0	4	1	1	1	0	0	0	1	0	2	3	26, 30
<i>Centroceras gasparrinii</i> BR2 DQ458919	0	3	1	1	1	0	0	0	1, 2	0	2	3	*, 1
<i>Centroceras gasparrinii</i> Morocco AF439294	0	3	1	1	1	0	0	?	?	?	?	1	1
<i>Centroceras gasparrinii</i> South Africa DQ374320	0	4	1	1	1	0	0	0	1	0	2	2	26, 30
<i>Centroceras gasparrinii</i> South Korea AY945766	0	?	1	1	1	0	0	0	2	1	2	4	26, 30
<i>Centroceras gasparrinii</i> South Korea1 HM240515	0	4	1	1	1	0	0	0	1	0	0	4	28
<i>Centroceras gasparrinii</i> Croatia LR536401	0	3	1	1	1	0	0	0	1	0	0	1	25
<i>Centroceras hommersandii</i> DQ374322	0	4	1	1	0	0	0	0	2	2	2	2	28, 30
<i>Centroceras hyalacanthum</i> BE KP222803	0	3	1	1	0	0	0	0	0	0	2	0	20
<i>Centroceras hyalacanthum</i> US DQ37434	0	3	1	1	1	0	0	0	2	2	0	3	30
<i>Centroceras illaqueans</i> KP222802	0	3	1	1	1	0	0	–	–	–	–	0	20
<i>Centroceras micracanthum</i> BE KP222804	0	4	1	1	1	0	0	–	–	–	–	0	20
<i>Centroceras natalense</i> DQ374343	0	4	1	1	1	0	0	–	–	–	–	2	30, 33
<i>Centroceras rodmanii</i> DQ374333	0	3	1	1	1	0	0	0	2	2	0	5	30
<i>Centroceras</i> sp. 1 JM DQ022809	0	4	1	1	1	0	0	0	2	2	0	3	30
<i>Centroceras tetrachotomum</i> DQ374323	0	4	1	1	1	0	0	0	2	2	0	2	30
<i>Ceramieae</i> sp. 4 JAW 4446	0	0	2	0	2	0	0	–?	–?	–?	–?	7	*
<i>Ceramieae</i> sp. 3 MBB 156	0	1	2	0	2	0	0	–	–	–	–	2	*
<i>Ceramiu</i> aff. <i>diaphanum</i> 1 FR871400	0	1	2	0	2	0	0	0	1	1	0, 1	0	*, 24
<i>Ceramiu</i> aff. <i>diaphanum</i> 2 FR871399	0	1	2	0	2	0	0	0	0, 1	0	1	0	*, 24
<i>Ceramiu</i> <i>barbatum</i> FR871396	0	2	2	0, 1	2	0	?	?	2	1	2	1	*, 24
<i>Ceramiu</i> <i>botryocarpum</i> AF439288	0	1	2, 3	1	2, 3	0	0	0	?	2	?	0	15, 16
<i>Ceramiu</i> <i>ciliatum</i> FR871397	0	1	2	0	3	0	0	0	2	2	2	0	24
<i>Ceramiu</i> <i>cimbricum</i> 1 Ireland 211	0	0	2	0	2	0	0	0	1	1	2	0	*
<i>Ceramiu</i> <i>cimbricum</i> 2 Ireland 212	0	0	2	0	2	0	0	0	1	1	2	0	*
<i>Ceramiu</i> <i>connivens</i> LR031254	0	1	3	1	3	0	0	0	?	0	2	1	26
<i>Ceramiu</i> <i>derbesii</i> FR775778	0	?	2, 3	1	2	0	0	0	?	2	?	0	24
<i>Ceramiu</i> <i>deslongchampsii</i> AF439293	0	0	2	0	2	0	0	0	2	0	2	0	1, 15, 16
<i>Ceramiu</i> <i>diaphanum sensu</i> Harvey FR871401	0	1	2	0	2	0	0	0	0, 1	1	0	0	24
<i>Ceramiu</i> <i>echionotum</i> AF439313	0	2	2	0	2	0	0	0	0, 1	1	1	0	15, 16
<i>Ceramiu</i> <i>gaditanum</i> 1052	0	0	2	1	2	0	0	0	2	1	2	0	*, 15
<i>Ceramiu</i> <i>glandulosum</i> 322	1	1	3	1	3	0	0	0, 1	?	2	?	0	*, 15
<i>Ceramiu</i> <i>nodosum</i> LR031256	0	1	2	0	2	0	?	0	?	2	2	1	26
<i>Ceramiu</i> <i>nudiusculum</i> FR775780	0	0, 1	2	0	2	0	0	0	2	2	2	1	24
<i>Ceramiu</i> <i>pallidum</i> AF439292	0	1	2	1	2	0	0	0	2	2	2	0	15, 16
<i>Ceramiu</i> <i>rothianum</i> LR031258	0	1	2	0	2	0	?	0	2, 3	1	2	1	26
<i>Ceramiu</i> <i>secundatum</i> 1 New Zealand	0	1, 2	2, 3	1	2, 3	0	0	0	2	2	1	5	*, 15
<i>Ceramiu</i> <i>secundatum</i> 2 Wales AF439286	0	1, 2	2, 3	1	2, 3	0	0	0	2	1	2	0	15, 16
<i>Ceramiu</i> <i>secundatum</i> 3 IR AF439287	0	1, 2	2, 3	1	2, 3	0	0	0	2	1	2	0	15, 16
<i>Ceramiu</i> <i>shuttleworthianum</i> FR871404	0	0	2	0	2	0	0	0	2	1	2	0	15, 16
<i>Ceramiu</i> <i>siliquosum</i> FR871405	0	2	2	0	2	0	0	0	1	1	2	0	15, 24
<i>Ceramiu</i> sp. 4 SP 1562	0	1	2	1	2	0	?	–	–	–	–	0	*
<i>Ceramiu</i> sp. 5 IT FR871407	0	1	2	0	2	0	0	–	1	1	2	1	24
<i>Ceramiu</i> <i>strictum sensu</i> Harvey FR871408	0	1	2	0	2	0	0	0	2	1	2	0	*, 24
<i>Ceramiu</i> <i>tenuicorne</i> Baltic FR871409	0	0	2	0	2	0	0	–	–	–	–	0	*, 24
<i>Ceramiu</i> <i>virgatum</i> 496 AF439290	0	1	2, 3	1	2, 3	0	0	–	–	–	–	0	15, 16
<i>Corallophila atlantica</i> 1 BR 146	0	1	2	1	2	0	0	–	–	–	–	3	*
<i>Corallophila atlantica</i> 2 BR 458	0	1	2	1	2	0	0	–	–	–	–	3	*
<i>Corallophila eatoniana</i> Washington US AY945765	0	1	2	1	2	0	0	0	1	2	2	4	4
<i>Ceramieae</i> sp. 5 DQ458953	0	2	2	1	2	0	0	0	2	2	2	3	*, 1, 11
<i>Gayliella ardissoni</i> 1 DQ458946	0	0, 1	1	0	1	0	1	0	0, 1	0	1	3	1, 12
<i>Gayliella ardissoni</i> 2 DQ458944	0	0, 1	1	0	1	0	1	0	0, 1	0	1	3	1, 12
<i>Gayliella dawsonii</i> DQ458938	0	0	1	0	1	0	1	0	0, 1	0	0, 1, 2	3	1, 12



## APPENDIX 3. — Continuation.

Taxon/Characters	1	2	3	4	5	6	7	8	9	10	11	12	References
<i>Gayliella flaccida</i> AY945778	0	0	1	0	1	0	1	—	—	—	—	0	7
<i>Gayliella iemanja</i> DQ458936	0	0	1	0	1	0	1	0	0, 1	1	0, 1	3	1, 12
<i>Gayliella jolyana</i> DQ458941	0	0	1	0	1	0	1	0	1	1	0	3	1, 12
<i>Gayliella mazoyerae</i> AY945776	0	0	1	0	1	0	1	—	—	—	—	1	7
<i>Gayliella</i> sp. 4 BR MN105065	0	0, 1	1	0	1	0	1	0	0, 1	1	0	3	12
<i>Gayliella tamoiensis</i> MN105075	0	0, 1	1	0	1	0	1	0	0, 1	1	0	3	12
<i>Gayliella taylorii</i> AY945774	0	0	1	0	1	0	1	?	?	?	?	4	7
<i>Gayliella transversalis</i> AY945777	0	0	1	0	1	0	1	0	1	1	0, 1	5	7
<i>Gayliella womersleyi</i> AY945780	0	1	1	0	1	0	1	0	1	1	2	5	7
<i>Herpochondria borealis</i> US1 424	1	1	2	1	2	1	0	0	2	2	1	4	*
<i>Herpochondria borealis</i> US2 EF613514	1	1	2	1	2	0	0	0	2	2	?	4	32
<i>Herpochondria corallinae</i> DQ787569	1	1	2	?	2	0	0	—	—	—	—	4	32
<i>Herpochondria elegans</i> AY945771	1	1	2	1	2	0	0	0	1	2	3	4	32
<i>Pseudocerarium</i> sp. 1 DQ458954	0	2	0	0	0	0	0	0	1	1	0	3	*, 1
<i>Pseudocerarium brevizonatum</i> 240	0	2	0	0	0	0	0	0	1	1	0	1	*
<i>Pseudocerarium caraibicum</i> AF259491	0	2	0	0	0	0	0	0	1	0	1	3	10
<i>Pseudocerarium clarionense</i> DQ458933	0	2	2	0	2	0	0	0	1	1	0	3	1, 2
<i>Pseudocerarium inkyuui</i> AF521801	0	1	2	0	2	0	0	0	1	1	2	4	10
<i>Pseudocerarium oliveirae</i> DQ458932	0	2	0	0	0	0	0	0	1	1	0	3	*, 1
<i>Pseudocerarium paniculatum</i> AF521802	0	1	2	0	2	0	—	0	1	1	2, 3	4	9, 10
<i>Pseudocerarium planum</i> 413	0	2	3	1	?	1	?	?	1	1	1	2	*, 22
<i>Pseudocerarium tenerrimum</i> AF521805	0	1	0	0	?	0	0	0	?	?	2, 3	4	10
<i>Reinboldiella filicula</i> AU DQ458956	0	1	2	0	2	0	0	0	2	1	1	5	1
<i>Reinboldiella filicula</i> BR DQ458942	0	1	2	0	2	0	—	0	1	1	1	3	*, 1
<i>Reinboldiella orientalis</i> Taiwan LC201458	1	1	2	1	2	0	1	1	2	2	4	4	21
<i>Reinboldiella schmitziana</i> JA LC201465	?	1	2	1	2	0	1	1	2	2	4	4	13, 14, 23
<i>Reinboldiella schmitziana</i> KO AY945772	0	1	3	1	2	0	1	—	—	—	—	4	13, 14, 23
<i>Reinboldiella taiwanensis</i> Taiwan LC201467	1	1	2	1	2	0	1	1	2	2	4	4	23
<i>Reinboldiella warburgii</i> TW1 EF125878	1	1	—	1	—	0	—	1	1	2	3	4	14
<i>Reinboldiella warburgii</i> TW2 LC201471	1	1	2	1	2	0	1	1	2	2	4	4	14
<i>Seiospora interrupta</i> AF439310	0	4	0	2	0	0	0	2	0	0	0	0	15, 17
<i>Spermothamniom repens</i> U04024	0	4	0	2	0	0	1	2	0	0	0	0	
<i>Sphondylothamniom multifidum</i> AF439312	0	4	0	2	0	0	0	2	0	0	0	0	15, 17
<i>Spyridia filamentosa</i> AF458705	0	1, 4	2	3	2	0	0	0	2	0	0	3	15, 17
<i>Stirkiella brasiliensis</i> DQ458922	0	1	2	0	2	0	0	0	1	1	1	3	*, 1
<i>Stirkiella codicola</i> AY155522	0	1	3	1	2	0	0	0, 1	1	2	?	4	6, 9
<i>Stirkiella coulteri</i> 402	0, 1	1	2	1	2	0	0	0	1	2	2	4	*
<i>Stirkiella dumoserta</i> GQ252454	0	1	2	0	2	0	?	2	2	1	1, 2	4	19
<i>Stirkiella fujiana</i> DQ458949	0	1	2	0	2	0	0	0	2	1	3	2	*, 1
<i>Stirkiella incospicua</i> LR031255	0	1	2	0	2	0	0	0	2	1	2	1	26
<i>Stirkiella interrupta</i> US AY155527	0	1, 2	2	0	2	0	0	0	1	2	2	4	6
<i>Stirkiella juliae</i>	0	1	2	0	2	0	0	0	0	0	0	5	*, 18
<i>Stirkiella pacifica</i> GQ179817	0	0, 1	2	0	2	0	0	0, 1	2	2	2	4	4
<i>Stirkiella riosmenae</i> JN712693	0	1	3	1	2	0	0	0	2	2	2	4	29
<i>Stirkiella sinicola</i> AY155531	0	1	3	0, 1	2	0	0	0, 1	1	2	2	4	6
<i>Stirkiella</i> sp. BR 110	0	1	2	0	2	0	0	—	—	—	—	3	*
<i>Stirkiella vaga</i> BR 126	0	1	2	0	2	0	0	0	1	1	2	3	*
<i>Yoneshigunea affinis</i> 1 DQ458920	0	0	0	0	0	0	0	0	0	0	0	3	*, 3
<i>Yoneshigunea affinis</i> 2 AF521797	0	0	0	0	0	0	0	—	—	—	—	4	12
<i>Yoneshigunea compta</i> BR 118	0	0	0	0	0	0	0	0	1	1	1	3	*

## APPENDIX 3 CHARACTER NAMES AND STATES

### 1. Thalli

- 0: terete
- 1: compressed

### 2. Number of periaxial

- 0: 4-6
- 1: 6-8
- 2: 8-10
- 3: 10-12
- 4: 12- more

### 3. Cortical initial cells

- 0: two
- 1: three
- 2: four
- 3: five

### 4. Cortication

- 0: partial
- 1: complete
- 2: none
- 3: complete in main axis

### 5. Descending filaments

- 0: none
- 1: one
- 2: two
- 3: three

### 6. Internal rhizoidal filaments

- 0: absent
- 1: present

### 7. Rhizoids

- 0: pluricellular
- 1: unicellular

### 8. Tetrasporangial origin

- 0: periaxial cells
- 1: cortical cells
- 2: axial cells

### 9. Tetrasporangial number

- 0: one
- 1: 2-3
- 2: 4-more

### 10. Exposure of tetrasporangia

- 0: naked
- 1: covered by cortical cells
- 2: immersed in thalli

### 11. Position of tetrasporangia

- 0: unilateral
- 1: bilateral
- 2: whorled spaced
- 3: whorled in stichidia- like

### 12. Geographic distribution

- 0: North Atlantic
- 1: Mediterranean
- 2: South Atlantic
- 3: Tropical Atlantic
- 4: North Pacific
- 5: South Pacific
- 6: Tropical Pacific
- 7: Tropical Indian Ocean

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APPENDIX 4. — Selected evolutionary models for the different partitioned data sets, best scores and tree length. Modelfinder (IQtree) using the BIC criterion. Bayesian inference under mixed models and unlinked rates.

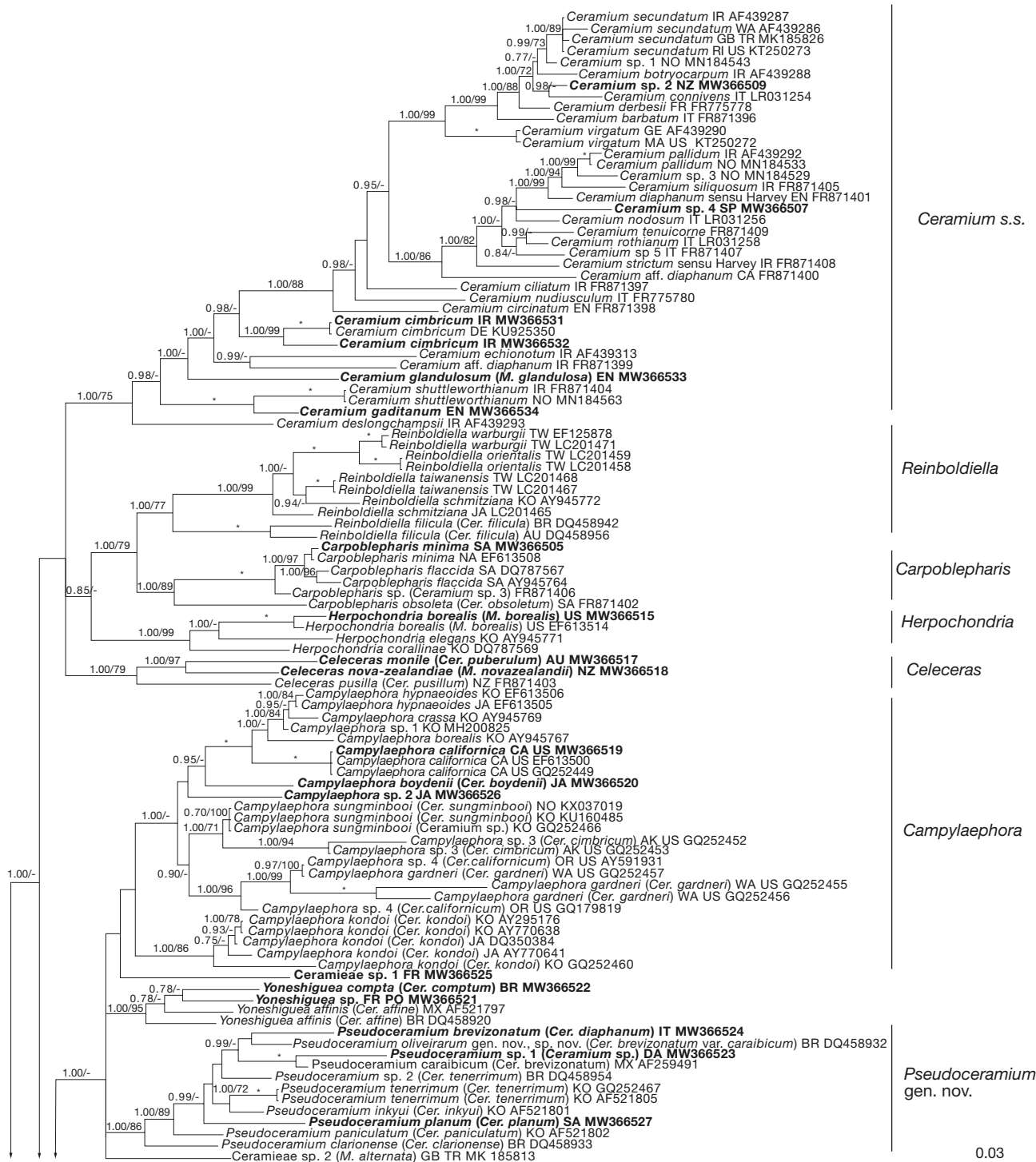
Alignments	Modelfinder (IQtree)			Bayesian Inference (MrBayes 3.2)
	IQ-TREE Web Server		IQ-TREE Terminal	
	Partitioned	Merging partitions	Merging partitions	
<i>rbcL</i> dataset 1139bp GY + F + R7				
codon 1	TIMe + R4	part1 + part2 SYM + R3	–	Unlinked parameters across partitions. Mixed models for each partition. Rate multiplier = Dirichlet (1.00, 1.00, 1.00); topologies equally probable a priori, and branch lengths = Unconstrained: Gamma Dir (1.0, 0.1000, 1.0, 1.0). Were similar for the codon positions. 1 = HKY; 2 = HKY; 3 = GTR
codon 2	TNe + R3	part1 + part3 GTR + F + R5	–	
codon 3	TIM2 + F + R4	part2 + part3 TIM + F + R5	–	
–	–	part1 + part2 + part3 GTR + F + R5	TIM + F + R4	
Optimal log-likelihood	-25310.603	-26438.943	-26462.317	-27944.90 (run1) -27968.84 (run2)
Total tree length	8.2873	5.249	5.307	–
Log-likelihood of consensus tree	-2783.275	-26439.887	-26462.549	–
COI-5P 624bp GY + F + G4				
codon 1	SYM + I + G4	GTR + F + I + G4	–	HKY
codon 2	TIM + F + I + G4	K3Pu + F + R3	–	HKY
codon 3	TN + F + I + G4	TIM + F + G4	–	GTR
Optimal log-likelihood	-12202.671	-12305.548	–	-13268.67 (run1) -13276.06 (run2)
Total tree length	30.883	18.510	–	–
Log-likelihood of consensus tree	-12092.794	-12307.528	–	–



APPENDIX 5. — Selected evolutionary models for the different data sets, best scores and tree length. Modelfinder (IQtree) using the BIC criterion. Bayesian inference under mixed models and unlinked rates.

Alignments	Modelfinder (IQtree)	Bayesian Inference (MrBayes 3.2)
LSU 573bp		
Optimal log-likelihood	TVMe+I+G4 -2780.932	NST=mixed rates=invgamma -2843.72 (run1) -2845.15 (run2)
Total tree length	0.959	—
Log-likelihood of consensus tree	-2783.275	—
<i>rbcL</i> _LSU_COI-5P combined data set 2487bp		
<i>rbcL</i> codon 1	TIM+F+R3	gtrsubmodel{3}[121221] referring to HKY
<i>rbcL</i> codon 2	TNe+F+I+G4	model
<i>rbcL</i> codon 3	TIM3+F+I+G4	
LSU	SYM+R3	—
COI-5P codon 1	SYM+I+G4	—
COI-5P codon 2	TIM3+F+I+G4	—
COI-5P codon 3	TIM2+F+I+G4	—
Optimal log-likelihood	-23560.397	-23958.45 (run1) -23968.57 (run2)
Total tree length	12.527	—
Log-likelihood of consensus tree	-23565.295	—
Integrative analyses <i>rbcL</i> (1249bp) + morphology (11 characters)		
<i>rbcL</i>	GTR+F+R5:part1+part2+part3	NST=6
Optimal log-likelihood	-22470.7653	States=4 rates=invgamma -23450.72 (run1) -23454.83 (run2)
Total tree length	4.4656	—
Log-likelihood of consensus tree	—	—
Morphology	MK+FQ+ASC+G4	Coding=variable
Optimal log-likelihood	-442.9161	States=equal rates=gamma -23450.72 (run1) -23454.83 (run2)
Total tree length	16.9323	—
Log-likelihood of consensus tree	-441.329706	—

FIGURE S1. — Phylogenetic reconstruction of the red algal tribe Ceramieae inferred from *rbcl* gene sequences (Part 1). The tree is the majority rule consensus tree resulting from Bayesian analysis. Values at the nodes represent posterior probability and bootstrap values for ML, support lower than 0.70 (PP) and 75 (BP) are not shown. Sequences generated in this study are in **bold**. Abbreviations: See Figure 3. Symbol: \*, full support.



0.03

FIGURE S2. — Phylogenetic reconstruction of the red algal tribe Ceramieae inferred from *rbcL* gene sequences (Part 2). The tree is the majority rule consensus tree resulting from Bayesian analysis. Values at the nodes represent posterior probability and bootstrap values for ML, support lower than 0.70 (PP) and 75 (BP) are not shown. Sequences generated in this study are in **bold**. Abbreviations: See Figure 3. Symbol: \*, full support.

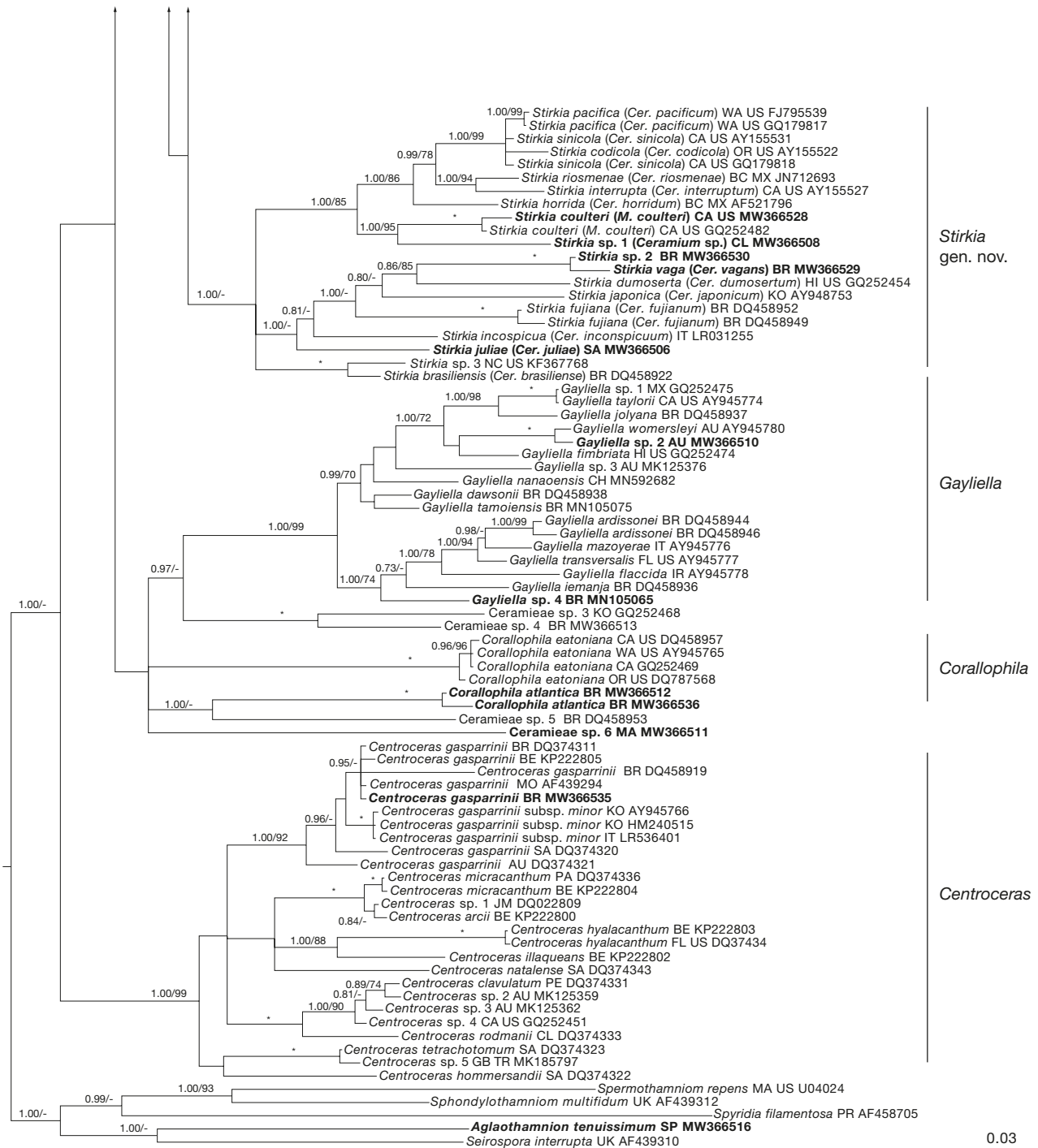
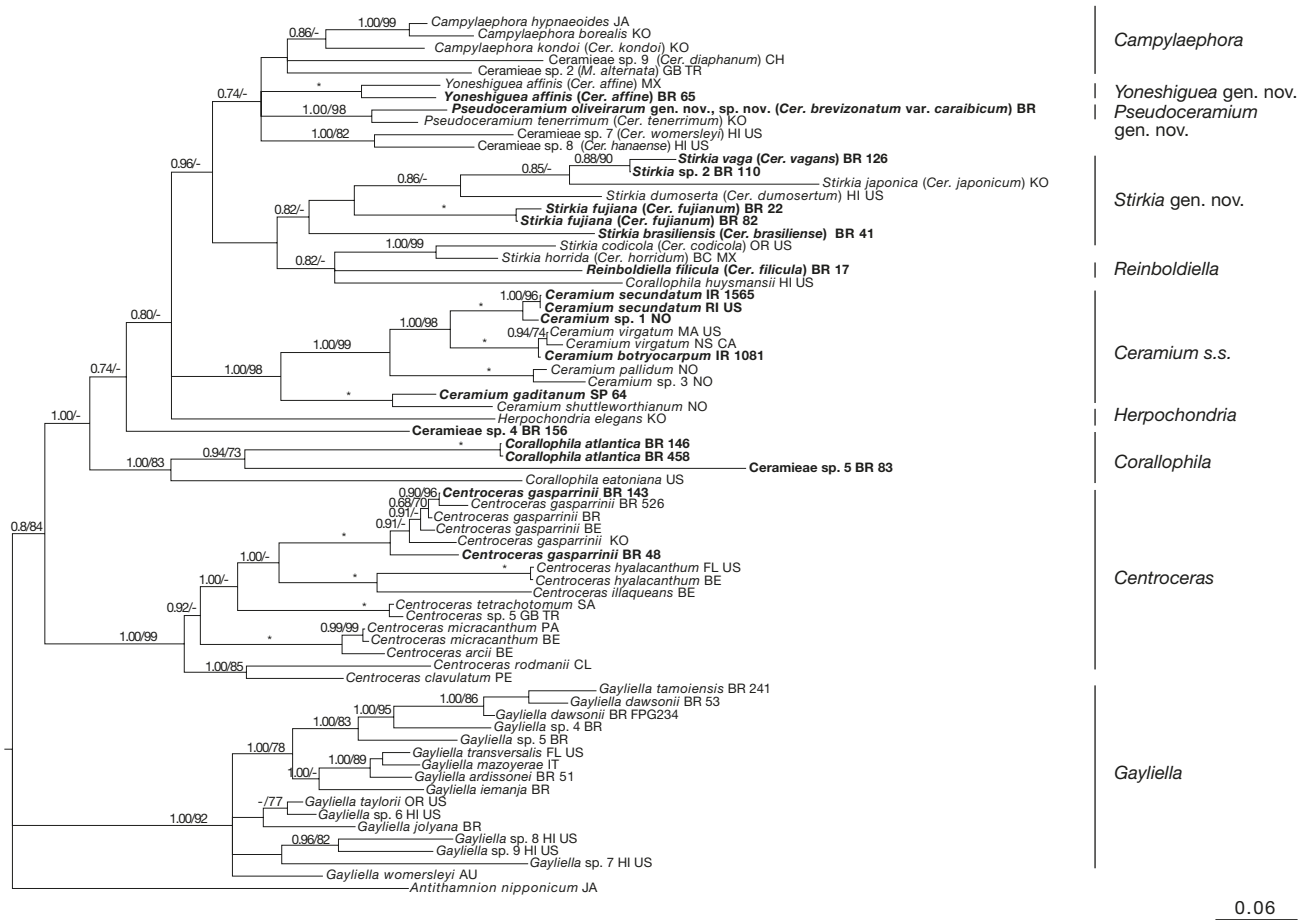


FIGURE S3. — Reconstructed phylogeny of Ceramieae based on concatenated *rbcl*, LSU and COI-5P gene sequences. Majority rule consensus tree resulting from Bayesian analysis. Values at the nodes represent posterior probability and bootstrap values for ML, support lower than 0.70 (PP) and 75 (BP) are not shown. Sequences generated in this study are in **bold**. Abbreviations: See Figure 3. Symbol: \*, full support.



0.06



FIGURE S4. — Bayesian tree inferred from partial LSU gene. The trees are the majority rule consensus tree resulting from Bayesian analysis. Values at the nodes represent posterior probability and bootstrap values for ML, support lower than 0.70 (PP) and 75 (BP) are not shown. Sequences generated in this study are in **bold**. Abbreviations: See Figure 3. Symbol: \*, full support.



FIGURE S5. — Bayesian tree inferred from COI-5P sequences. The trees are the majority rule consensus tree resulting from Bayesian analysis. Values at the nodes represent posterior probability and bootstrap values for ML, support lower than 0.70 (PP) and 75 (BP) are not shown. Sequences generated in this study are in **bold**. Abbreviations: See Figure 3. Symbol: \*, full support.

