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Thea R. POPOLIZIO, Craig W. SCHNEIDER, Walter M. JONGBLOED,
Gary W. SAUNDERS & Christopher E. LANE

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Molecular analysis resolves the taxonomy of the *Laurencia* complex (Rhodomelaceae, Ceramiales) in Bermuda and uncovers novel species of *Chondrophyucus* and *Laurenciella*

Thea R. POPOLIZIO

Department of Biology, Salem State University, Salem, Massachusetts, 01970 (United States)
tpopolizio@salemstate.edu (corresponding author)

Craig W. SCHNEIDER
Walter M. JONGBLOED

Department of Biology, Trinity College, Hartford, Connecticut, 06106 (United States)

Gary W. SAUNDERS

Centre for Environmental & Molecular Algal Research, Department of Biology,
University of New Brunswick, Fredericton, NB E3B 5A3 (Canada)

Christopher E. LANE

Department of Biological Sciences, University of Rhode Island, Kingston,
Rhode Island, 02881 (United States)

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ABSTRACT

In the last decade, molecular tools have revealed a significant number of previously unrecognized taxa in Bermuda's marine flora, especially among the Rhodophyta. A number of species have been persistently misidentified based on morphological similarities to species described from other localities. Some have been assigned to existing taxa not previously reported for the islands, and many have been determined to be novel species. Of late, researchers have substantially modified the '*Laurencia* complex' in several regions around the globe. Herein, we confirm the presence in Bermuda of five of the eight genera recognized in this complex – *Laurencia* J.V.Lamouroux, *Chondrophyucus* (J.Tokida & Y.Saito) Garbary & J.T.Harper, *Palisada* (Yamada) K.W.Nam, *Yuzurua* (K.W.Nam) Martin-Lescanne and *Laurenciella* Cassano, Gil-Rodríguez, Senties, Díaz-Larrea, M.C.Oliveira & M.T.Fujii, and discuss the species historically and presently known in the islands. Both *rbcL* chloroplast sequences and COI-5P mitochondrial sequences support the recognition of at least two species for what has historically been labeled *L. obtusa* in Bermuda, these assigned to *L. dendroidea* J.Agardh and *L. catarinensis* Cordeiro-Marino & M.T.Fujii in molecular analyses. We present two new species, *Chondrophyucus planiparvus* Popolizio, C.W.Schneider & C.E.Lane, sp. nov. and *Laurenciella namii* Popolizio, C.W.Schneider & C.E.Lane, sp. nov., the latter genetically distinct from *L. marilzae* (Gil-Rodríguez, Senties, Díaz-Larrea, Cassano & M.T.Fujii) Gil-Rodríguez, Senties, Díaz-Larrea, Cassano & M.T.Fujii, *L. mayaimii* Collado-Vides, Cassano & M.T.Fujii and an undescribed species from Brazil. We also used ITS (rRNA) sequences to explore species limits for *Laurencia catarinensis*, *L. dendroidea* and *L. microcladia* Kützing. A full description of *Laurencia microcladia*, based on recent collections from Bermuda and the Caribbean Sea, is also included in this study.

KEY WORDS
Bermuda,
COI-5P,
ITS,
rbcL,
Rhodomelaceae,
new species.

RÉSUMÉ

L'analyse moléculaire résout la taxonomie du complexe Laurencia (Rhodomelaceae, Ceramiales) aux Bermudes et permet la découverte de nouvelles espèces de Chondrophyucus et Laurenciella.

Au cours de la dernière décennie, les outils moléculaires ont révélé un nombre important de taxons précédemment non reconnus dans la flore marine des Bermudes, en particulier parmi les Rhodophytes. Un certain nombre d'espèces ont été constamment mal identifiées sur la base de similitudes morphologiques avec des espèces décrites dans d'autres localités. Certaines ont été attribuées à des taxons existants qui n'avaient pas été signalés auparavant pour les îles, et beaucoup ont été déterminées comme étant des espèces nouvelles. Ces derniers temps, les chercheurs ont considérablement modifié le « complexe *Laurencia* » dans plusieurs régions du monde. Dans cet article, nous confirmons la présence aux Bermudes de cinq des huit genres reconnus dans ce complexe – *Laurencia* J.V.Lamouroux, *Chondrophyucus* (J.Tokida & Y.Saito) Garbary & J.T.Harper, *Palisada* (Yamada) K.W.Nam, *Yuzurua* (K.W.Nam) Martin-Lescanne et *Laurenciella* Cassano, Gil-Rodríguez, Senties, Díaz-Larrea, M.C.Oliveira & M.T.Fujii, et nous discutons des espèces historiquement et actuellement connues dans les îles. Les séquences chloroplastiques *rbcL* et les séquences mitochondriales COI-5P soutiennent la reconnaissance d'au moins deux espèces pour le matériel qui a été historiquement étiqueté *L. obtusa* aux Bermudes, celles-ci étant assignées à *L. dendroidea* J.Agardh et *L. catarinensis* Cordeiro-Marino & M.T.Fujii dans les analyses moléculaires. Nous présentons deux nouvelles espèces, *Chondrophyucus planiparvus* Popolizio, C.W.Schneider & C.E.Lane, sp. nov. et *Laurenciella namii* Popolizio, C.W.Schneider & C.E.Lane, sp. nov., cette dernière étant génétiquement distincte de *L. marilzae* (Gil-Rodríguez, Senties, Diaz-Larrea, Cassano & M.T.Fujii) Gil-Rodríguez, Senties, Diaz-Larrea, Cassano & M.T.Fujii, *L. mayaimii* Collado-Vides, Cassano & M.T.Fujii et d'une espèce non décrite du Brésil. Nous avons également utilisé les séquences ITS (rRNA) pour explorer les limites des espèces pour *Laurencia catarinensis*, *L. dendroidea* et *L. microcladia* Kützing. Une description complète de *Laurencia microcladia*, basée sur des collections récentes des Bermudes et de la mer des Caraïbes, est également incluse dans cette étude.

MOTS CLÉS
Bermudes,
COI-5P,
ITS,
rbcL,
Rhodomelaceae,
espèces nouvelles.

INTRODUCTION

The '*Laurencia* complex' is a diverse sub-grouping of red algae in the family Rhodomelaceae (Tribe Laurencieae Schmitz 1889) found in tropical and temperate seas worldwide and contains 232 currently accepted species (Guiry & Guiry 2020). In the past several decades, this group has received substantial attention from phycologists around the world due to its convoluted taxonomy and nomenclature (e.g., Fujii *et al.* 2006; Cassano *et al.* 2009, 2012b; Martin-Lescanne *et al.* 2010; Metti *et al.* 2015). Within the complex (and in addition to *Laurencia sensu stricto*) the genus *Osmundea* Stackhouse has been resurrected (Nam *et al.* 1994), *Chondrophyucus* (J.Tokida & Y.Saito) Garbary & J.T.Harper (Garbary & Harper 1998) and *Yuzurua* (K.W.Nam) Martin-Lescanne (Martin-Lescanne *et al.* 2010) have been elevated to generic status, and four new genera have been described – *Palisada* (Yamada) K.W.Nam (Nam 2007), *Laurenciella* Cassano, Gil-Rodríguez, Senties, Díaz-Larrea, M.C.Oliveira & M.T.Fujii (Cassano *et al.* 2012b), *Corynecladia* J.Agardh (Metti *et al.* 2015; Cassano *et al.* 2019) and *Obelopapa* F.Rousseau, Martin-Lescanne, Payri & L.Le Gall (Rousseau *et al.* 2017). Members of the '*Laurencia* complex' are known to exhibit considerable morphological plasticity, making them challenging to diagnose using morphology alone. Each of the genera, however, has been shown to form well-supported monophyletic clades in multiple publications, except for the taxon-rich genus *Laurencia* (138 spp.). This group is in need of extensive molecular and morphological analysis and, likely, additional re-organization.

As a genus, *Laurencia* Kützing has already been significantly modified by molecular-assisted alpha taxonomy (MAAT) (e.g. Gil-Rodríguez *et al.* 2009; Cassano *et al.* 2012a, b; Collado-Vides *et al.* 2018). Erected by Lamouroux (1813: 131-132) for only eight species, *L. obtusa* (Hudson) J.V.Lamouroux was later lectotypified as the generic type (Schmitz 1889). In his monograph of *Laurencia*, Yamada (1931) separated the genus into four sections based on morphological and anatomical features. Saito (1967) segregated *Laurencia sensu lato* into two subgenera, designating these *Chondrophyucus* and *Laurencia* based on differences in tetrasporangial arrangement and the presence or absence of secondary pit connections. Decades later, the genus *Osmundea* (Stackhouse 1809) was resurrected by Nam *et al.* (1994) within the complex and distinguished from *Laurencia* by the reproductive characters of tetrasporangial and spermatangial branch origin. By this time, it was also established that *Laurencia* possessed four pericentral cells, whereas the other genera had only two. Using morphological cladistics, Garbary & Harper (1998) elevated the subgenus *Chondrophyucus* to generic rank as sister to *Osmundea* based primarily on the presence of two (rather than four) pericentral cells in vegetative axes and trichoblast-type spermatangial development. *Osmundea* exhibits filament-type spermatangial development. Many of the species nested within the *Chondrophyucus* clade resolved by Garbary & Harper (1998) have since been transferred to *Palisada*, a genus proposed and later validated by Nam (2007) based on Yamada's (1931) section *Palisadae* of *Laurencia*, with tetrasporangial development unique from that of *Chondrophyucus*. Martin-Lescanne *et al.*

(2010) segregated *Yuzurua* from *Palisada sensu stricto* on molecular evidence, adding a fifth genus to the complex. The authors determined the morphological traits of *Yuzurua* to mainly overlap with those of *Palisada*, but with secondary pit connections between cortical cells in the former, and lacking the characteristic palisade-like cells of the latter genus. The genus *Laurenciella* was added to the complex for a molecularly distinct clade that is entirely morphologically cryptic with its sister genus *Laurencia sensu stricto* (Cassano *et al.* 2012b). The genus *Corynecladia* (as *Coronaphycus* Metti) was recognized for an independent clade that included *Laurencia elata* (C.Agardh) Hooker f. & Harvey and is morphologically characterized by development of an extensive secondary cortex at the base of the thallus (Metti *et al.* 2015). The name was emended to *Corynecladia* when molecular evidence placed *C. elata* (C.Agardh) Cassano, M.C.Oliveira & M.T.Fujii and *C. nova* (Metti) Cassano, M.C.Oliveira & M.T.Fujii in a clade with the generitype *Corynecladia clavata* (Sonder) J.Agardh (Cassano *et al.* 2019). Most recently, *Laurencia flexilis* Setchell (Rousseau *et al.* 2017) was designated as the generitype *Ohelopapa flexilis* F.Rousseau, Martin-Lescanne, Payri & L.Le Gall for a new genus (Rousseau *et al.* 2017), creating a further subdivision in the *Laurencia* complex.

Members of the *Laurencia* complex are distinguished from the closely related genus *Chondria* C.Agardh by both vegetative and reproductive characters. *Chondria* displays five pericentral cells per axial cell (often only obvious at the apices); genera in the *Laurencia* complex produce either two or four (Womersley 2003). Spermatangial plates form in *Chondria*; alternatively, in the *Laurencia* complex male gametangia develop from trichoblasts located within apical pits (Nam 1999).

Several workers in the past two decades have provided a phylogenetic basis for the re-organization of the *Laurencia* complex within a broad global context and have introduced a great number of new or reinstated genera (Cassano *et al.* 2009; Gil-Rodríguez *et al.* 2009; Martin-Lescanne *et al.* 2010). Comprehensive surveys of this complex using molecular tools are less common for specific localities like Bermuda, but the results are particularly interesting when compared to historical accounts of the islands' flora. Reports of *Laurencia* in Bermuda first appeared in the literature in the mid 19th century, the earliest by Alexander F. Kemp (1857), who included *L. obtusa* and *L. papillosa* C.Agardh (now *Palisada perforata* (Bory) K.W.Nam). *Laurencia obtusa* (type locality = England) was subsequently recorded from the islands by workers over the next century (Rein 1873; Dickie 1874; Hemsley 1884; Murray 1888; Collins *et al.* 1916 [as *Phycotheca Boreali-Americana* XLII, no. 2092]; Collins & Hervey 1917; Howe 1918; Tandy 1936; Bernatowicz 1952) followed by later 20th century accounts (see Schneider 2003). *Laurencia obtusa* var. *crucifera* Kützing was reported by Dickie (1874), and var. *gracilis* (C.Agardh) Zanardini by Collins & Hervey (1917). Collins & Hervey (1917) reported *L. paniculata* J.Agardh from Bermuda, and this species is presently regarded as a junior synonym of *L. obtusa*. Rein (1873) provided the first account of *Yuzurua poiteaui* (J.V.Lamouroux) Martin-Lescanne (as *L. gemmifera* Harvey). Howe (1918) included *L. intricata* J.V.Lamouroux, *L. microcladia* Kützing, and *Palisada corallopsis*

(Montagne) Senties, M.T.Fujii & Díaz-Larrea [as *L. corallopsis* (Montagne) M.Howe] in his survey of the islands' flora. Almost a century later, Schneider & Lane (2005, 2007) and Schneider *et al.* (2010) added *L. decumbens* Kützing, *Yuzurua iridescens* (M.J.Wynne & D.L.Ballantine) Senties, M.J.Wynne, Cassano, Gil-Rodríguez & M.T.Fujii [as *Chondrophyucus iridescens* (M.J.Wynne & D.L.Ballantine) Garbary & J.T.Harper] and *L. caraibica* P.C.Silva to the Bermuda flora.

The present study provides the molecular and morphological evidence needed to establish *Laurencia dendroidea* J.Agardh, *L. catarinensis* Cordeiro-Marino & M.T.Fujii, *Palisada flagellifera* (J.Agardh) K.W.Nam, and novel species of *Laurenciella* and *Chondrophyucus* as constituents of the *Laurencia* complex in the Bermuda flora. We also verify previous reports of the following members of this tribe: *Laurencia intricata* J.V.Lamouroux, *L. microcladia* Kützing, *Palisada perforata* (Bory) K.W.Nam, *P. corallopsis*, *Yuzurua poiteaui* (J.V.Lamouroux) Martin-Lescanne and *Y. iridescens*, and distinguish the formerly synonymized *P. cervicornis* (Harvey) Collado-Vides, Cassano & M.T.Fujii from *P. corallopsis* in Bermuda. Unfortunately, our attempts to obtain sequence data from archival material of *L. caraibica* and *L. decumbens* collected in Bermuda in the recent past have been unsuccessful.

METHODS

Collections were made in shallow water (0-3 m) or via scuba (to 23 m), and site locations were taken using a Garmin™ eTrex H (Olathe, Kansas, United States). A portion of each specimen used for DNA analysis was dried on silica gel, and the remainder of the thallus was pressed onto herbarium paper as a permanent voucher. Selected fragments were preserved in 4-5% formaldehyde in seawater for anatomical study. Sections were mounted in 30% corn syrup with acidified 1% aniline blue in a ratio of 20:1 with a few drops of formaldehyde as a medium preservative. Live specimens chosen for DNA analysis were photographed using a Canon Powershot s90 digital camera (Canon Inc., Tokyo, Japan), and dried herbarium specimens were scanned on an HP 309a Photosmart Premium scanner (Hewlett-Packard Company, Palo Alto, California, United States). Photomicrographs were taken using Zeiss Axioskop 40 microscope (Oberkochen, Germany) equipped with a model 11.2 Spot InSight 2 digital camera (Diagnostic Instruments, Sterling Heights, Michigan, United States). The digital images were composed in Adobe Photoshop™ CS6 v. 13.0.1 (Adobe Systems, San Jose, California, United States). Voucher specimens of some numbers are deposited in KIRI, MICH, NY, the Bermuda Natural History Museum (BAMZ) and Herbarium C.W. Schneider. Herbarium abbreviations follow the online *Index Herbariorum* (<http://sweetgum.nybg.org/ih/>) and standard author initials are from Brummitt & Powell (1992). The *Phycotheca Boreali-Americana* (P.B.-A.) exsiccata cited here is part of CWS' personal herbarium.

Silica-dried samples for DNA analysis were ground in liquid nitrogen and stored at -20°C. DNA was extracted from 0.1-0.5 µl ground material using a GenElute Plant Genomic

Miniprep Kit according to manufacturer protocol (Sigma-Aldrich, St. Louis, Missouri, United States) with 500 µl of modified lysis solution (50 µl 10% TWEEN 20, and 5 µl of 20 mg/ml Proteinase K added), as well as 1 hr 23°C incubation followed by a 20 min incubation on ice (Saunders & Druehl 1993).

DNA was amplified via polymerase chain reaction (PCR) with the Takara Ex-Taq DNA polymerase kit (PanVera, Madison, WI, United States) in an Eppendorf AG Mastercycler epGradient thermal cycler (Eppendorf, Hamburg, Germany). To assign all specimens to species groups, two oligonucleotide primers were used for both sequencing and amplification of the COI-5P barcode marker (the 5' region of the cytochrome *c* oxidase subunit I gene), GWSFn (Le Gall & Saunders 2010) and GWSRx (Saunders & McDevit 2012). A denaturation cycle of 94°C for 4 min was followed by 38–42 cycles of 94°C for 1 min, 45°C for 1 min, 72°C for 1 min and a final extension of 72°C for 7 min. Several specimens were selected for additional sequencing of the plastid-encoded RuBisCO (*rbcL*) operon. Four oligonucleotide primers were used for both amplification and sequencing of two overlapping fragments: forward- RR1 (5' ATGTCTAACTCTGTAGAAG 3') and reverse- RR4 (5' TTCAGTCTTTTCATACAT 3') and forward- RrIf (5' TCTCAGCCTTTTATGCGTTG 3') and reverse- Rrr (5' ATCTCACTATTCTATACTCC 3'). A denaturation cycle of 94°C for 4 min was followed by 35 cycles of 94°C for 1 min, 47°C for 1 min, 72°C for 2 min, and a final extension of 72°C for 7 min. Amplified DNA was treated with the QIAquick PCR Purification Kit following the manufacturer's protocol (Qiagen Redwood City, California, United States), and the purified PCR product was sequenced at the Rhode Island Genomics and Sequencing Center using the Applied Biosystems Inc. 3130xl Genetic Analyzer (Life Technologies, Grand Island, New York, United States). Specimens used in COI-5P and *rbcL* analyses are recorded in Appendix 1.

To compare intraspecific vs. interspecific sequence distances in three of our *Laurencia* taxa, allowing us to assess species boundaries not clearly resolved with COI-5P and *rbcL*, we sequenced the internal transcribed spacer region of nuclear ribosomal cistron (ITS). ITS amplification and sequencing followed Saunders & Moore (2013) using the primers P1 and Harv4 for amplification and sequencing, as well as the internal primers P5 and R1 for sequencing. The resulting 18 ITS sequences were aligned using MUSCLE (multiple sequence comparison by log-expectation) in Geneious Prime (v. 2020.1 available from <http://www.geneious.com>) and adjusted by eye where needed. Sequence comparison for the ITS was based only on nucleotide substitutions between/among species with the insertions and deletions (indels) removed prior to barcode gap analysis. Specimens used in ITS analysis are recorded in Appendix 2.

COI-5P sequences from representative species within the *Laurencia* complex, including those available through GenBank and newly determined here (Appendix 1), were included in an alignment using MUSCLE (in Geneious v. 9.0.5). The COI-5P alignment was analyzed in Geneious using the Species Delimitation tool to calculate intraspecific variation and nearest neighbor distances (barcode gap) (Table 1). To compare intraspecific variation and nearest neighbor distances in a second gene, we repeated the alignment and distance analysis described above using *rbcL* sequence data from our collected specimens and from GenBank (Appendix 1 and Table 1). These data were used to demarcate genetic species groups.

Following barcode gap analyses, an alignment was constructed with MUSCLE (in Geneious v. 9.0.5) using full-length *rbcL* (the RuBisCO large subunit gene) sequences for one representative of each genetic species. In some instances, multiple specimens from our collections representing the same species were included in the analysis because they were from different geographic locations (i.e., Bermuda, Florida and/or the Caribbean). To place our western Atlantic specimens in a broader context, all relevant GenBank data (Appendix 1) for the *Laurencia* complex were added to the alignment (generated using MUSCLE in Geneious v. 9.0.5), along with several other taxa in the Rhodomelaceae as outgroups. The best model of evolution for the *rbcL* (132 taxa, 1217 sites) was determined in jModelTest 2 (volume 2.1.10; Darriba *et al.* 2012). The selected phylogenetic model (GTR+I+G) was used to complete maximum likelihood (ML) and Bayesian (BI) analyses. In both analyses the data set was partitioned by codon. The *rbcL* maximum likelihood phylogeny was estimated using the RAxML graphical user interface (Silvestro & Michalak 2012) with branch support calculated using 1000 bootstrap replicates. Bayesian analysis of *rbcL* was conducted in MrBayes v.3.2.2 (Ronquist & Huelsenbeck 2003) and run with four parallel chains of the Markov chain Monte Carlo (three heated + one cold) starting with a random tree and sampling at intervals of 1000 generations for four million generations. After 1 million generations the standard deviation of split frequencies reached 0.01 and likelihood scores had stabilized, thus the initial 1000 trees were discarded as the burn-in. Posterior probabilities (PP) were estimated based on the remaining trees. The generated tree was manipulated for presentation (Fig. 1) using FigTree v1.4.4 software (<http://tree.bio.ed.ac.uk/software/figtree/>).

RESULTS/SYSTEMATICS

Our DNA barcode (COI-5P) analysis included 243 sequences (ranging from 458 to 617 base pairs [bp]) from members of the *Laurencia* complex; 170 of these (70%) were generated for this study from specimens collected in Bermuda, the

Fig. 1. — Maximum likelihood tree topology derived from analysis of *rbcL* sequences with bootstrap values (≥ 70) and Bayesian posterior probabilities (≥ 0.95) appended, respectively. A dash (-) indicates values lower than these thresholds for that analysis, while an asterisk (*) indicates strong support ($>98/1$) for both metrics. Branches leading to an unsupported node (i.e., support values below the ML and BI thresholds) are colored **gray**. Sequences from taxa appearing in boldface type were newly generated in this study.

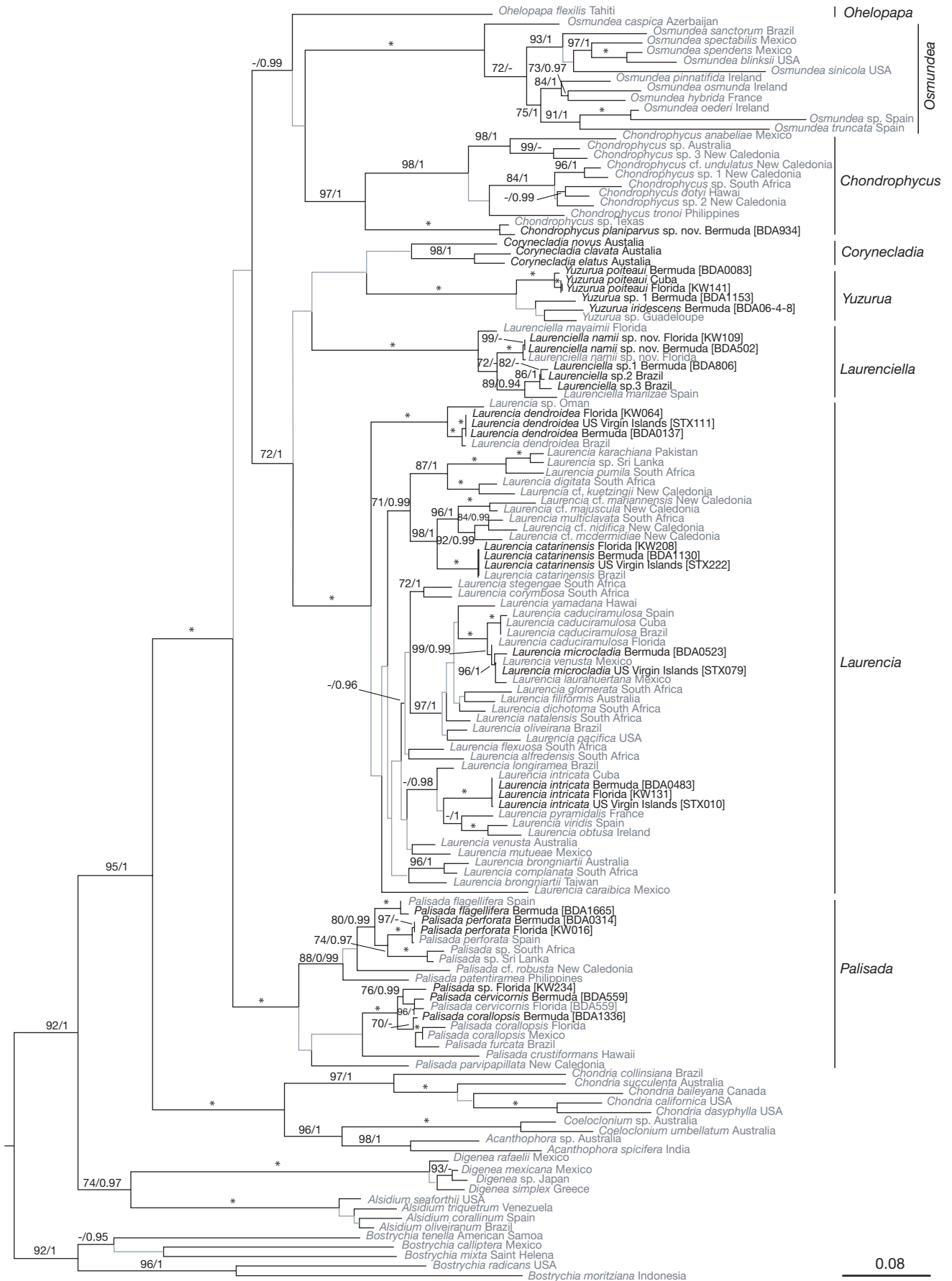


TABLE 1. — Intraspecific divergence and distance to nearest neighbor in COI-5P and *rbcL* for taxa within the *Laurencia* complex included in this study. a-Includes *Chondrophycus* sp. (Texas) b-Includes *Laurencia* sp. (Sri Lanka) c-Includes taxa currently ascribed to *L. venusta* (Mexico), *L. caduciramulosa* (United States) and *L. laurahuertana*. When these sequences are excluded, the maximum intraspecific divergence for *L. microcladia* is 0.4%. d-Includes *Laurenciella* sp. 2 (Brazil) * Species with new sequence data from collections made in Bermuda, St. Croix, and/or the Florida Keys. For both COI-5P and *rbcL* genes, we selected one specimen of each newly sequenced species and geographic location for deposit in GenBank. The complete datasets for each gene can be shared upon request.

| Species | COI-5P | | | | | <i>rbcL</i> | | | |
|---------------------------------|--------|-----------------------------------|--------------------------------|----------------------------------|----|----------------------------------|-------------------------------|----------------------------------|--|
| | n | Max intra-specific divergence (%) | Nearest neighbor | Distance to nearest neighbor (%) | n | Max intraspecific divergence (%) | Nearest neighbor | Distance to nearest neighbor (%) | |
| <i>Chondrophycus</i> | — | — | — | — | — | — | — | — | |
| <i>C. dotyi</i> | 1 | — | <i>C. planiparvus</i> sp. nov. | 9.3 | 1 | — | <i>C. sp. 1</i> South Africa | 3.8 | |
| <i>C. planiparvus</i> sp. nov.* | 1 | — | <i>C. undulatus</i> | 8.8 | 2a | 0.5 | <i>C. sp. Australia</i> | 9.5 | |
| <i>C. undulatus</i> | 4 | 0.4 | <i>C. planiparvus</i> sp. nov. | 8.8 | 1 | — | <i>C. sp. 1</i> New Caledonia | 2.1 | |
| <i>Corynecladia</i> | — | — | — | — | — | — | — | — | |
| <i>C. clavata</i> | 1 | — | <i>O. flexilis</i> | 10.5 | 1 | — | <i>C. elatus</i> | 2.5 | |
| <i>Laurencia</i> | — | — | — | — | — | — | — | — | |
| <i>L. catarinensis</i> * | 24 | 0.5 | <i>L. karachiana</i> | 5.2 | 6 | 0.06 | <i>L. majuscula</i> | 4.2 | |
| <i>L. dendroidea</i> * | 60 | 2.4 | <i>L. intricata</i> | 9.3 | 7 | 0.5 | <i>L. longiramea</i> | 5.5 | |
| <i>L. intricata</i> * | 10 | 0.1 | <i>L. longiramea</i> | 5.2 | 8 | 0.3 | <i>L. longiramea</i> | 3.7 | |
| <i>L. karachiana</i> | 1 | — | <i>L. catarinensis</i> | 5.2 | 2b | 0.3 | <i>L. pumila</i> | 2.1 | |
| <i>L. longiramea</i> | 1 | — | <i>L. pacifica</i> | 4.2 | 1 | — | <i>L. pyramidalis</i> | 2.9 | |
| <i>L. mcdermidiae</i> | 4 | 0.8 | <i>L. intricata</i> | 7.9 | 1 | — | <i>L. nidifica</i> | 2.5 | |
| <i>L. microcladia</i> * | 19 | 0.5 | <i>L. nidifica</i> | 4.6 | 5c | 0.5 | <i>L. caduciramulosa</i> | 1.2 | |
| <i>L. nidifica</i> | 5 | 1.2 | <i>L. microcladia</i> | 4.6 | 1 | — | <i>L. mcdermidiae</i> | 2.5 | |
| <i>L. nipponica</i> | 3 | 0.4 | <i>L. satoi</i> | 3.7 | — | — | — | — | |
| <i>L. obtusa</i> | 1 | — | <i>L. viridis</i> | 2.8 | 1 | — | <i>L. viridis</i> | 2.0 | |
| <i>L. pacifica</i> | 2 | 0.3 | <i>L. longiramea</i> | 4.2 | 1 | — | <i>L. catarinensis</i> | 7.3 | |
| <i>L. pyramidalis</i> | 4 | 0.3 | <i>L. longiramea</i> | 6.2 | 2 | 0.08 | <i>L. viridis</i> | 3.3 | |
| <i>L. satoi</i> | 1 | — | <i>L. nipponica</i> | 3.7 | 1 | — | — | — | |
| <i>L. viridis</i> | 3 | 0.2 | <i>L. obtusa</i> | 2.8 | 2 | 0.5 | <i>L. obtusa</i> | 1.8 | |
| <i>Laurenciella</i> | — | — | — | — | — | — | — | — | |
| <i>L. marilzae</i> | 3 | 1.1 | <i>L. sp. 1Bda</i> | 6.0 | 3 | 0.4 | <i>L. sp. 3</i> Brazil | 1.6 | |
| <i>L. mayaimii</i> | 1 | — | <i>L. marilzae</i> | 8.7 | 1 | — | <i>L. namii</i> sp. nov. | 3.6 | |
| <i>L. namii</i> sp. nov.* | 14 | 0.4 | <i>L. mayaimii</i> | 9.4 | 3 | 0.2 | <i>L. marilzae</i> | 3.9 | |
| <i>L. sp. 1Bda</i> * | 1 | — | <i>L. marilzae</i> | 6.0 | 2d | 0.4 | <i>L. sp. 3</i> Brazil | 0.9 | |
| <i>Ohelopapa</i> | — | — | — | — | — | — | — | — | |
| <i>O. flexilis</i> | 1 | — | <i>C. clavata</i> | 10.5 | 1 | — | <i>L. mcdermidiae</i> | 12.5 | |
| <i>Osmundea</i> | — | — | — | — | — | — | — | — | |
| <i>O. hybrida</i> | 1 | — | <i>O. pinnatifida</i> | 7.1 | 2 | 0.6 | <i>O. pinnatifida</i> | 5.1 | |
| <i>O. osmunda</i> | 1 | — | <i>O. pinnatifida</i> | 5.7 | 2 | 0.05 | <i>O. pinnatifida</i> | 4.6 | |
| <i>O. spectabilis</i> | 6 | 0.8 | <i>O. hybrida</i> | 9.7 | 4 | 0.3 | <i>O. splendens</i> | 4.2 | |
| <i>O. splendens</i> | 2 | 0.5 | <i>O. pinnatifida</i> | 12.1 | 3 | 0.6 | <i>O. blinksii</i> | 1.7 | |
| <i>O. pinnatifida</i> | 1 | — | <i>O. osmunda</i> | 5.7 | 3 | 0.2 | <i>O. osmunda</i> | 4.6 | |
| <i>Palisada</i> | — | — | — | — | — | — | — | — | |
| <i>P. cervicornis</i> * | 2 | 0 | <i>Palisada</i> | 4.5 | 3 | 0.7 | <i>P. sp. 1</i> Fla | 2.0 | |
| <i>P. corallopsis</i> * | 2 | 0 | <i>Palisada</i> | 3.9 | 4 | 0.6 | <i>P. furcata</i> | 2.1 | |
| <i>P. flagellifera</i> * | 6 | 1.3 | <i>P. parvipapillata</i> | 6.3 | 5 | 0.2 | <i>P. perforata</i> | 3.0 | |
| <i>P. parvipapillata</i> | 1 | — | <i>P. flagellifera</i> | 6.3 | — | — | — | — | |
| <i>P. perforata</i> * | 28 | 0.6 | <i>P. flagellifera</i> | 6.7 | 16 | 0.2 | <i>P. sp. South Africa</i> | 2.6 | |
| <i>P. sp. 1Fla</i> * | 3 | 0 | <i>P. corallopsis</i> | 3.9 | 3 | 0.0 | <i>P. cervicornis</i> | 2.0 | |
| <i>Yuzurua</i> | — | — | — | — | — | — | — | — | |
| <i>Y. iridescens</i> * | 2 | 0 | <i>Y. poiteaui</i> | 6.9 | 3 | 0.0 | <i>Y. sp. Guadeloupe</i> | 3.7 | |
| <i>Y. poiteaui</i> * | 11 | 0.8 | <i>Yuzurua</i> | 5.7 | 10 | 0.2 | <i>Y. sp. Guadeloupe</i> | 5.3 | |
| <i>Y. sp. 1Bda</i> * | 1 | — | <i>Y. poiteaui</i> | 5.7 | 1 | — | <i>Y. iridescens</i> | 4.4 | |

Florida Keys and St. Croix, USVI. The remaining 73 COI-5P sequences were downloaded from GenBank (Appendix 1). Maximum intraspecific divergence for COI-5P based on our data combined with sequences available in GenBank ranged from 0-1.3% for all species except *Laurencia dendroidea* (2.4%; Table 1). Interspecific variation for COI-5P ranged from 2.8-12.1% (Table 1). To compare distance values for a second gene in the same set of species, we combined *rbcL* sequences (*n* = 111) from our collections with additional data from GenBank (Appendix 1). Maximum intraspecific divergence for *rbcL* ranged from 0-0.7%, while interspecific variation ranged from 0.9-9.5% (Table 1).

The DNA barcode analysis allowed us to organize our large data set into 15 distinct genetic species groupings (Table 1). Of these 15 genetic groups, ten can be assigned to currently reported species of *Laurencia* (*L. catarinensis*, *L. dendroidea*, *L. intricata* and *L. microcladia*), *Palisada* (*P. cervicornis*, *P. corallopsis*, *P. flagellifera* and *P. perforata*) and *Yuzurua* (*Y. iridescens* and *Y. poiteaui*). Two are novel species described herein, *Chondrophycus planiparvus* Popolizio, C.W.Schneider & C.E.Lane, sp. nov. and *Laurenciella namii* Popolizio, C.W.Schneider & C.E.Lane, sp. nov. The three remaining genetic groups were assigned provisional names pending further study, viz., *Laurenciella* sp. 1Bda, *Palisada* sp. 1 USA and *Yuzurua* sp. 1Bda.

TABLE 2. — Intraspecific ITS divergence and distance to nearest neighbor for 3 species in the genus *Laurencia* J.V.Lamouroux

| Species | Max intraspecific divergence (%) | Nearest neighbor | Distance to nearest neighbor (%) |
|-------------------------------|----------------------------------|------------------------------|----------------------------------|
| <i>Laurencia microcladia</i> | 2.0 | <i>Laurencia dendroidea</i> | 29.2 |
| <i>Laurencia catarinensis</i> | 2.1 | <i>Laurencia dendroidea</i> | 32.6 |
| <i>Laurencia dendroidea</i> | 0.6 | <i>Laurencia microcladia</i> | 29.2 |

We had no genetic groups that were a morphological match to *L. caraibica* or *L. decumbens*, species that are also reported for Bermuda.

To further explore the separation between intra- and inter-specific sequence variability in a subset of taxa, we selected specimens of *Laurencia catarinensis*, *L. dendroidea* and *L. microcladia* and compared distance values for the ITS region of nuclear rRNA (Appendix 2; Table 2). The 18 ITS sequences generated were unusually long for red algae (~2700 bp) with relatively low levels of variation within species. After removing indels from the alignment (~1000 bp) the maximum intraspecific ITS divergences were lowest among Bermuda *L. dendroidea* (0.6%; Table 2), while sequences of *L. catarinensis* from Bermuda had 2.0% divergence (Table 2). Sequences of *L. microcladia* from both Bermuda and St. Croix displayed 2.1% divergence (Table 2), just slightly more than *L. catarinensis* despite representing a broader geographical sampling. Comparatively, interspecific ITS distances between the three species ranged from 29.2–32.6% (Table 2).

For phylogenetic analyses in the complex, the *rbcl* gene was selected given the extent of molecular studies using this gene in the past decade. To place our genetic groups into a phylogenetic context, a representative of each of the previously determined groups was included in a single gene (*rbcl*) analysis (1217 bp) along with a diverse representation of taxa assigned to the complex for which data were mined from GenBank (Appendix 1). Phylogenetic associations among genera in the tribe conformed largely to those published by Metti *et al.* (2015), Rousseau *et al.* (2017) and Cassano *et al.* (2019). Our analysis similarly provides robust support for the generic groupings in the complex, except *Corynecladia* (as in previous studies), which may be partly due to the small number of species in the genus relative to other genera (Fig. 1). Relationships between genera, however, are not supported. Our tree topology depicts the sister relationships of *Laurencia-Laurenciella* [as in Cassano *et al.* (2019) and Rousseau *et al.* (2017)], *Osmundea-Chondrophyucus* [as in Cassano *et al.* (2019) and Metti *et al.* (2015)] and *Corynecladia-Yuzurua* (as in the three publications mentioned previously) (Fig. 1). But none of the analyses, including ours, generated branch values to support these relationships. Phylogenies from the previous studies depict *Palisada* as sister to the *Laurencia-Laurenciella-Yuzurua-Corynecladia* clade, with poor support in all except for the Bayesian inference results of Rousseau *et al.* (2017). Similarly, the *Palisada* clade resolved as a strongly supported generic grouping in our analysis, but its relationship to other members of the complex remains unresolved.

Finally, the monospecific *Ohelopapa* groups with *Osmundea* and *Chondrophyucus* in our phylogeny, a result upheld only by the Bayesian analysis (Fig. 1). Previous phylogenetic studies show different, poorly supported relationships of *Ohelopapa* with other genera in the complex.

After our barcode gap and phylogenetic analyses, new species in *Chondrophyucus* and *Laurenciella* are added to the flora of the western Atlantic Ocean. We further discovered several species previously unknown for Bermuda, and these are herein added to the island flora. Due to the lack of a comprehensive description of *Laurencia microcladia* from the western Atlantic, we provide one here for specimens collected in Bermuda and the U.S. Virgin Islands at the northern end of the West Indies (type locality, “*ex India occidentali*”; Kützing 1865).

Family RHODOMELACEAE Horaninow
Genus *Laurencia* J.V.Lamouroux

Laurencia microcladia Kützing
(Figs 2, 3)

Tabulae phycologicae : 22, pl. 60, figs b, c (1865).

DISTRIBUTION. — Bermuda, Florida, Central America, Caribbean, Brazil, Mediterranean, Azores, Canary Islands, Cape Verde Islands, North Africa, Arabian Gulf, Singapore, Vietnam, Polynesia, Samoa (Guiry & Guiry 2021).

DESCRIPTION

Plants to 6.5 cm tall, fleshy, green to deep purplish-red, often with distinct purple-red branchlet tips, forming clumps with several associated upright axes; individual axes narrowly pyramidal or sometimes with secondary branches not varying much in length from base to tip of main axes; main axes to 0.5 mm diam. with discoidal holdfasts; densely irregularly branched in all directions, some branches clustered creating a whorled appearance; branchlets clavate to narrowly turbinate, to 2 mm long; densely clustered ultimate branches imparting a verrucose appearance. Vegetative axes with 4 pericentral cells; secondary pit connections present; in surface view cortical cells 15–50 µm diam., irregularly rounded to rounded rectangular in upper branch regions, elongate-angular to elongate-ovoid below; *corps en cerise* present; outer cortical cell projections absent. In transverse section, outer cortical cells appearing subquadrate or campanulate to ovoid, 12–36 µm diam.; medullary cells 45–120 µm diam. Branch tips with deep apical pits, trichoblasts emerging from the pits, dichotomously branched

to 6 or more orders, and expanding in diam. distally. Tetrasporangia arranged parallel to axis (Saito 1967, p. 71), spherical to slightly ovoid, 60–100 µm diam. (Fig. 3B, C); cystocarps urn-shaped, situated near branchlet tips, 600–820 µm diam. (Fig. 3D), carposporangia obpyriform, 30–60 µm diam. and 80–125 µm long. Spermata formed in dense fascicles issued from lower portions of trichoblasts, spherical to obovoid, 2–3 µm diam.

Genus *Laurenciella* V.Cassano, Gil-Rodríguez, Senties, Díaz-Larrea, M.C.Oliveira & M.T.Fujii

Laurenciella namii

Popolizio, C.W.Schneider & C.E.Lane, sp. nov.
(Fig. 4)

HOLOTYPE. — *Craig W. Schneider (CWS)/Christopher E. Lane (CEL)/Thea R. Popolizio (TRP)* 12-11-2 [BDA0597] (Fig. 4B), 18.I.2012, Spanish Point Park, north shore Bermuda I., Bermuda, western Atlantic Ocean, 32°18'26.4"N, 64°48'56.6"W, depth 0–2 m [deposited in MICH]; isotypes – Bermuda Natural History Museum (BAMZ), Herb. CWS [BDA0598] (Fig. 4A), NY, UNB.

HOLOTYPE DNA BARCODE. — GenBank OK209887, COI-5P.

PARATYPES. — **Bermuda.** *CWS/CEL/TRP* 10-16-12 [BDA0227], 21.VIII.2010, Whalebone Bay, St. George's I., 32°21'51.0"N, 64°42'43.5"W, depth 1 m; *CWS/CEL/TRP* 10-33-13 [BDA0502] (see Appendix 1); *CWS/CEL/TRP* 10-33-15 [BDA0504], 25.VIII.2010, Spanish Point Park, *loc. cit.*, depth 2 m; *CWS/CEL/TRP* 12-8-1 [BDA0544], 17.VI.2012, Brackish Pond Flats, north shore Bermuda I., 32°21'07.0"N, 64°48'02.5"W, depth 3–4 m; *TRP/CWS* 12-143-4 [BDA1591], 25.X.2012, Trunk I., Harrington Sound, 32°19'58.7"N, 64°43'33.9"W, depth 1–2 m; *CWS/TRP* 13-20-4 [BDA1871], 18.IX.2013, Whalebone Bay, *loc. cit.*, depth 1 m. **Florida.** *CWS/CEL/TRP/DCM* 13-9-5 [KW109] (see Appendix 1); *CWS/CEL/TRP/DCM* 13-9-17 [KW125], 29.V.2013, Key West, White St. Pier, 24°32'45.4"N, 81°47'00.0"W, depth 2 m; *CWS/CEL/TRP/DCM* 13-9-25 [KW133], White St. Pier, *loc. cit.*, depth 2 m; *CWS/CEL/TRP/DCM* 13-14-7 [KW219], 31.V.2013, Cudjoe, Summerland Bridge, 24°39'39.0"N, 81°26'10.9"W, depth 1–3 m.

EPONOMY. — An honorific name for Professor Ki Wan Nam of Pukyong National University, Korea, who has played a significant role in the taxonomic diversification of the *Laurencia* complex using both morphological and phylogenetic data.

DISTRIBUTION. — Bermuda and Florida, United States.

SEASONALITY. — Collected throughout the year in Bermuda.

DESCRIPTION

Plants to 15 cm tall with main axes yellow-orange and deep red branchlets (Fig. 4A), fleshy; main axes lax, slender, to 1 mm diam., suboppositely to alternately spiraled branching and arising from discoidal holdfasts. Mature axes in lower portions, elongated and lacking branchlets, appearing denuded (Fig. 4A); upper portions demonstrating profuse alternate to irregular branching (Fig. 4C); ultimate branchlets cylindrical to clavate, to 2 mm long and 140–350 µm in diam. Vegetative axes with 4 pericentral cells; secondary pit connections present in cortical cells; cortical cells in surface view 20–45 µm diam., irregularly rounded-polygonal to ovoid, becoming

more elongated in lower portions of branches, outer cortical cells often appearing obpyriform at branch apices; *corps en cerise* present in living plants, one per outer cortical cell; outer cortical cells acutely projecting, the surface appearing crenate in longitudinal section (Fig. 4D, F). In transverse section, two layers of pigmented cortical cells with three inner layers of colorless irregularly globose medullary cells 30–115 µm diam., decreasing in size radially toward the cortex (Fig. 4E). In section, outer cortical cells rounded-rectangular to ovoid or campanulate, 25–40 µm diam. and 20–35 µm long. Deep apical pits at branch apices bearing dense trichoblast systems to 220 µm long with 3–4 orders of subdichotomous branching (Fig. 4F, G). Reproductive structures not found. Distinct from other species of *Laurenciella* by its COI-5P and *rbcL* molecular sequences.

Genus *Chondrophycus*

(J.Tokida & Y.Saito) Garbary & J.T.Harper

Chondrophycus planiparvus

Popolizio, C.W.Schneider & C.E.Lane, sp. nov.
(Fig. 5)

HOLOTYPE. — *T.R. Popolizio/C.W. Schneider* 12-40-13 (BDA0934), 13.III.2012, Gurnet Rock, mouth of Castle Harbour, Bermuda, western Atlantic Ocean, 32°20'22.7"N, 64°39'44.8"W, depth 13 m [deposited in UNB]; iso-, MICH [*TRP* 12-40-12 (BDA0933)].

HOLOTYPE DNA BARCODE. — GenBank OK209884, COI-5P; OK209859, *rbcL*.

PARATYPES. — **Bermuda.** *CWS/CEL* 09-30-9, 19.III.2009, Gurnet Rock, *loc. cit.*, 32°20'20.2"N, 64°39'32.1"W, depth 16–17 m; *TRP/CWS* 12-148-6 [BDA1625], 5.XI.2012, wreck of the *Pelinaion*, north shore Bermuda I., 32°21'20.9"N, 64°38'36.9"W, depth 18 m; *TRP/CWS* 12-160-8 [BDA1741], 1.XII.2012, wreck of the *Hermes*, south shore Bermuda I., 32°14'42.4"N, 64°48'00.1"W, depth 23 m.

ETYMOLOGY. — From the Latin, describing the typical habit of this flattened ('*planus*') and relatively small ('*parvus*') species.

DISTRIBUTION. — Endemic to Bermuda as presently known.

SEASONALITY. — Collected from November to March in Bermuda.

DESCRIPTION

Plants to 2 cm high, distinctly compressed, rosy-red, cartilaginous (Fig. 5A–D); main axes to 2 mm diam. with one or more arising from discoidal holdfasts; branching irregular to opposite or alternate, with branch apices sometimes appearing trifurcated (Fig. 5B, D); branchlets to 2 mm in diam. Vegetative axes with 2 pericentral cells; cortical cells arranged longitudinally in surface view (Fig. 5E, H), secondary pit connections abundant (Fig. 5G, H). In transverse section, non-palisade outer cortical cells, obtriangulate to obovate, with constrictions at the base (Fig. 5G), 12–35 µm diam. and 9–27 µm long, some acute projections present at branch apices in surface view; outer cortical cells ovoid in upper branch regions, irregularly angular and elongated below, 9–55 µm diam. and 20–100 µm long (Fig. 5H); lenticular thickenings



FIG. 2. — *Laurencia microcladia* Kützinger: **A**, illustration of *L. microcladia* from Børgesen (1915, as *L. obtusa* var. *gelatinosa* (J.V.Lamouroux) J.Agardh) from the US Virgin Islands; **B**, Sequenced specimen of *L. microcladia* collected in St. Croix, USVI, Caribbean Antilles [CEL/TRP/EDS 13-26-2/STX079]. Scale bar: 2 mm.

absent in the walls of medullary cells. Extensive trichoblasts emerging from shallow apical pits (Fig. 5F), dichotomously branched, to 600 μm long. Tetrasporangia forming at api-

ces, slightly ovoid, arranged at right angles to the axis (Saito 1967: 71), 43-68 μm diam. and 48-96 μm long (Fig. 5I). Gametangia not found.

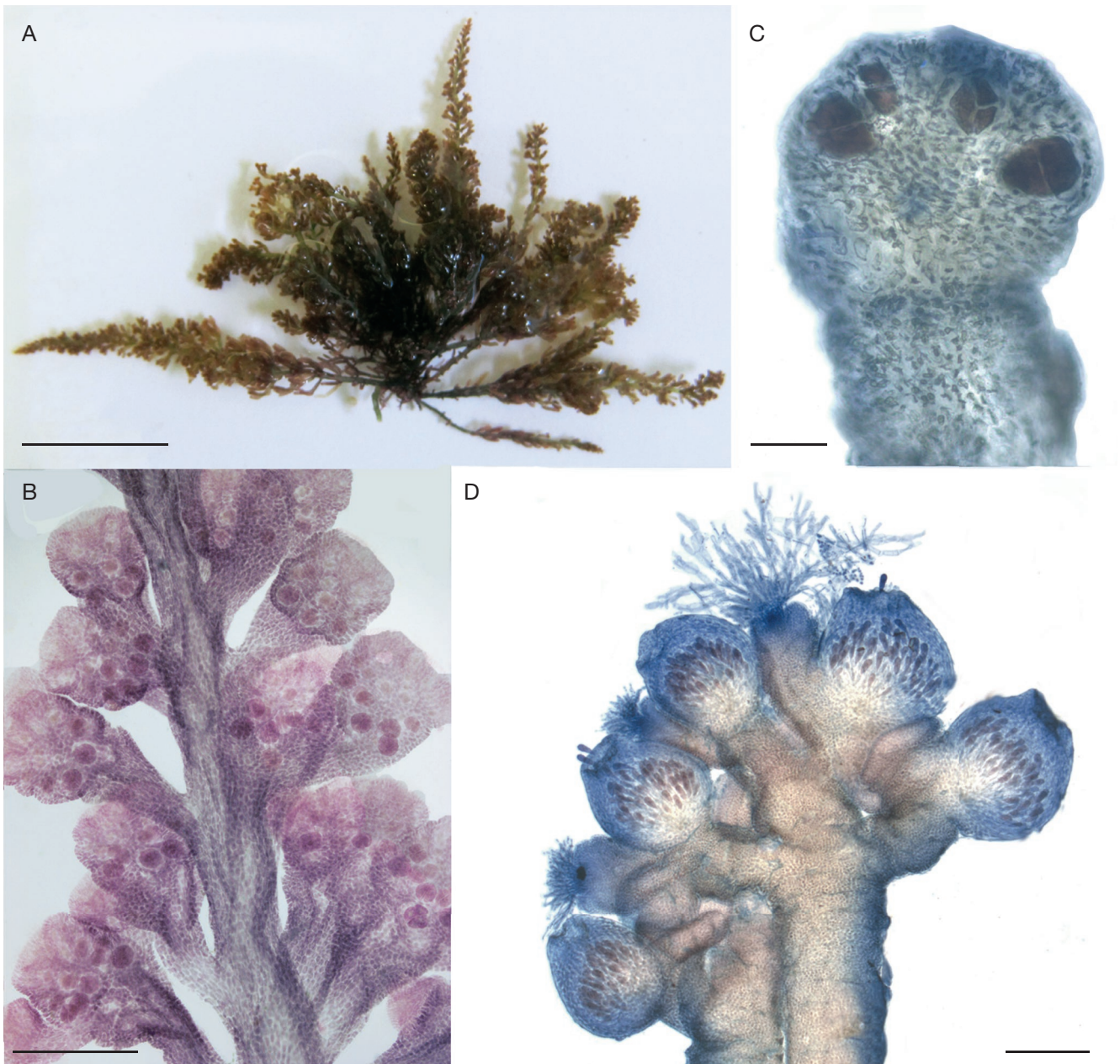


FIG. 3. — *Laurencia microcladia* Kützing: **A**, habit with clustered characteristic narrowly pyramidal axes [TRP 12-30-11/BDA0818]. **B**, whole mount of tetrasporic specimen, displaying irregular branching in all planes and parallel arrangement of tetrasporangia [CWS/CEL 03-21-1]; **C**, longitudinal section of branch tip showing parallel arrangement of tetrasporangia [TRP 12-172-3]; **D**, whole mount of female specimen illustrating clustered, urn-shaped cystocarps and obpyriform carposporangia [CWS/CEL 03-21-1]. Scale bars: A, 2 cm; B, C, 250 μ m; D, 500 μ m.

DISCUSSION

THE GENUS *LAURENCIA* IN BERMUDA

COI-5P and *rbcL* sequence data support the recognition of two species for collections long called *Laurencia obtusa* in Bermuda, both of which are distantly related to true *L. obtusa* from Europe. These species represent examples of western Atlantic entities with a misassigned European binomial placed upon them by phycologists of the 19th and early 20th centuries (see Popolizio *et al.* 2013). The *rbcL* barcode gap analysis presents support for the conspecific-

ity of Bermuda specimens with *Laurencia dendroidea* and *L. catarinensis* from Brazil (Cassano *et al.* 2012a; Machín-Sánchez *et al.* 2012). Intraspecific divergences in *rbcL* for the two are 0.5% and 0.3%, respectively, compared with interspecific divergences of 5.5% and 3.7% (Table 1). These species herein represent new reports for Bermuda. Our collections of these two species had previously been assigned to *L. obtusa*, but our molecular data suggest *L. obtusa* is not found in Bermuda and likewise may not be present in the tropical western Atlantic. These data also show that both species are present in the Florida Keys and St. Croix

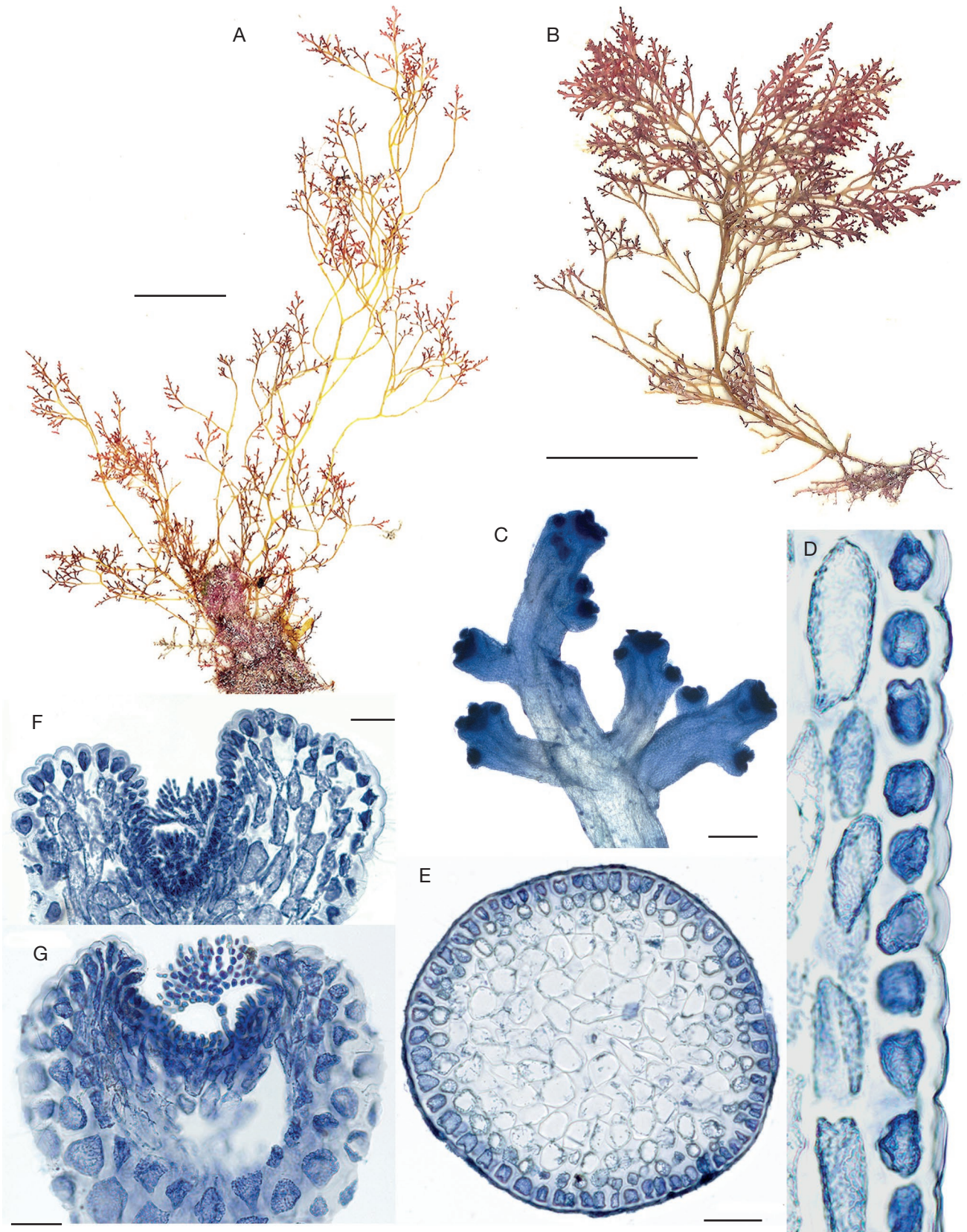


FIG. 4. — *Laurenciella namii* Popolizio, C.W.Schneider & C.E.Lane sp. nov. **A**, isotype specimen [CWS/CEL/TRP 12-11-2/BDA0598]; **B**, holotype specimen [CWS/CEL/TRP 12-11-2/BDA0597]; **C**, axial tip displaying irregular branching [CWS/CEL/TRP/DCM 13-9-17/KW125]; **D**, Longitudinal section of branch with outer cortical cells demonstrating a crenate margin [CWS/CEL/TRP/DCM 13-9-17/KW125]; **E**, transverse section of axis showing two outer layers of corticated pigmented cells and four inner layers of colorless, irregularly globose medullary cell layers [CWS/CEL/TRP/DCM 13-9-17/KW125]; **F**, longitudinal section of axial tip illustrating apical pit, trichoblasts and crenate outer margins [CWS/CEL/TRP/DCM 13-9-5/KW109]; **G**, longitudinal section of axial tip; orientation shows depth of apical pit and developing trichoblasts [CWS/CEL/TRP/DCM 13-9-17/KW125]. Scale bars: A, 2 cm; B, 1 cm; C, 500 µm; D, F, G, 50 µm; E, 100 µm.

TABLE 3. — Morphological character comparisons for treatments of *Laurencia microcladia* Kützing, *L. caduciramulosa* Masuda & S.Kawaguchi, *L. laurahuertana* Mateo-Cid, Mendoza-Gonzalez, Senties & Diaz-Larrea and *L. venusta* Yamada.

| | <i>Laurencia microcladia</i> | <i>Laurencia microcladia</i> | <i>Laurencia caduciramulosa</i> | <i>Laurencia caduciramulosa</i> | <i>Laurencia laurahuertana</i> | <i>Laurencia venusta</i> | <i>Laurencia venusta</i> |
|--|--|---|---|--|---|--|---|
| Location of specimens used for data | West Indies (type locality) | Bermuda | Vietnam (type locality) | Florida, United States | Caribbean Mexico (type locality) | Caribbean Mexico | Korea and Japan (type locality) |
| Thallus color | Gray-green to purple-green | Green to deep purple-red, often with distinct purple-red branchlet tips | Purple-red | Greenish-brown | Pale green | Pale green | Brown, greenish or purple red or brown with pink branch tips |
| Length of upright to axes (cm) | to 10 | to 6.5 | 2-5 | to 1 | to 0.7 | to 7 | to 10 |
| Branching pattern | Alternately to irregularly branched, dense distally | Alternately to irregularly branched, dense distally; some branches clustered, appearing whorled | Irregularly alternate and spirally arranged | Irregularly alternate and spirally arranged, usually with 2-3 orders of branches | Sparse, dichotomous below, irregularly alternate above | Sparse, verticillate, 2-4 branches per verticile, less commonly opposite, alternate or irregular | Irregularly alternate, subopposite or subverticillate; occasionally curved branches with secund ultimate branchlets |
| Outer cortex cell diam. (µm) on main axes | 30-60 | 15-50 | 10-30 distally, 20-36 proximally | 23-45 | Not reported | 14-52 | 33-58 |
| Outer cortex cross-sectional cell projection | Not reported | Absent | Slightly near branch apices | Present | Present (undulate) | Absent | Absent or slight |
| Tetrasporangial arrangement | Not reported | Parallel | Not reported | Not reported | Not reported | Parallel | Parallel |
| Tetrasporangia | Spherical to ovoid; 65-100 µm diam. | Spherical to slightly ovoid; 60-100 µm diam. | Not reported | Not reported | 60-65 µm diam. | 40-80 µm diam. | 75-86 µm diam. |
| Cystocarp shape | Spherical to urn-shaped; near branchlet tips | Urn-shaped, situated near branchlet tips | Not reported | Not reported | Urn-shaped | Prominent; laterally positioned to bearing branchlet; urn-shaped to conical | Urn-shaped to conical or ovoid without a protuberant ostiole |
| Cystocarp diam. (µm) | 500-700 | 600-820 | Not reported | Not reported | 450-500 | 400-600 | 600-870 |
| Carposporangia | Not reported | Obpyriform, 80-125 µm long, 30-60 µm diam. | Not reported | Not reported | Pyriform; 90-100 µm long, 22-25 µm diam. | 100-150 µm long, 30-50 µm diam. | Not reported |
| Spermatangia | Not reported | Spherical to ovoid; 4.5-10 µm diam.; sterile apical cells present | Not reported | Not reported | Ovoid, 11-13 µm long, 3-4 µm diam.; sterile apical cells absent | Ovoid; 6-11 µm long, 4-7 µm diam.; sterile apical cells present | Ovoid; 10-12 µm, 5-7 µm diam.; sterile apical cells present |
| References for data | Taylor 1960; Howe 1918; Littler & Littler 2000; Dawes & Mathieson 2008 | Present study | Masuda <i>et al.</i> 1997 | Collado-Vides <i>et al.</i> 2014 | Mateo-Cid <i>et al.</i> 2014 | Senties <i>et al.</i> 2001 | Yamada 1931; Saito 1967; Nam <i>et al.</i> 2000 |

in the US Virgin Islands. Notably, specimens we have identified as having “red” habits in our collections group only within the *L. dendroidea* clade, along with green and purple-green morphs of this species. All specimens that were noted as ‘green with pink tips’ in our field notes fall within the *L. catarinensis* clade. It is likely that Howe (1918) was examining collections of *L. catarinensis* when describing ‘*L. obtusa*’ from the islands as “subglobose tufts” that are “often greenish with red tips,” features that appear to char-

acterize the habit of this species based on our observations and genetic sequences.

The presence of *Laurencia intricata* in Bermuda also has been verified with molecular data. Sequence data show that this species, first reported for the islands by Howe (1918), is conspecific with specimens from the Caribbean Antilles, the type locality of this species. Intraspecific divergence values are 0.1% in COI-5P and 0.3% in *rbcL* (Table 1). We have discovered a specimen of *L. intricata* among Hervey’s archived

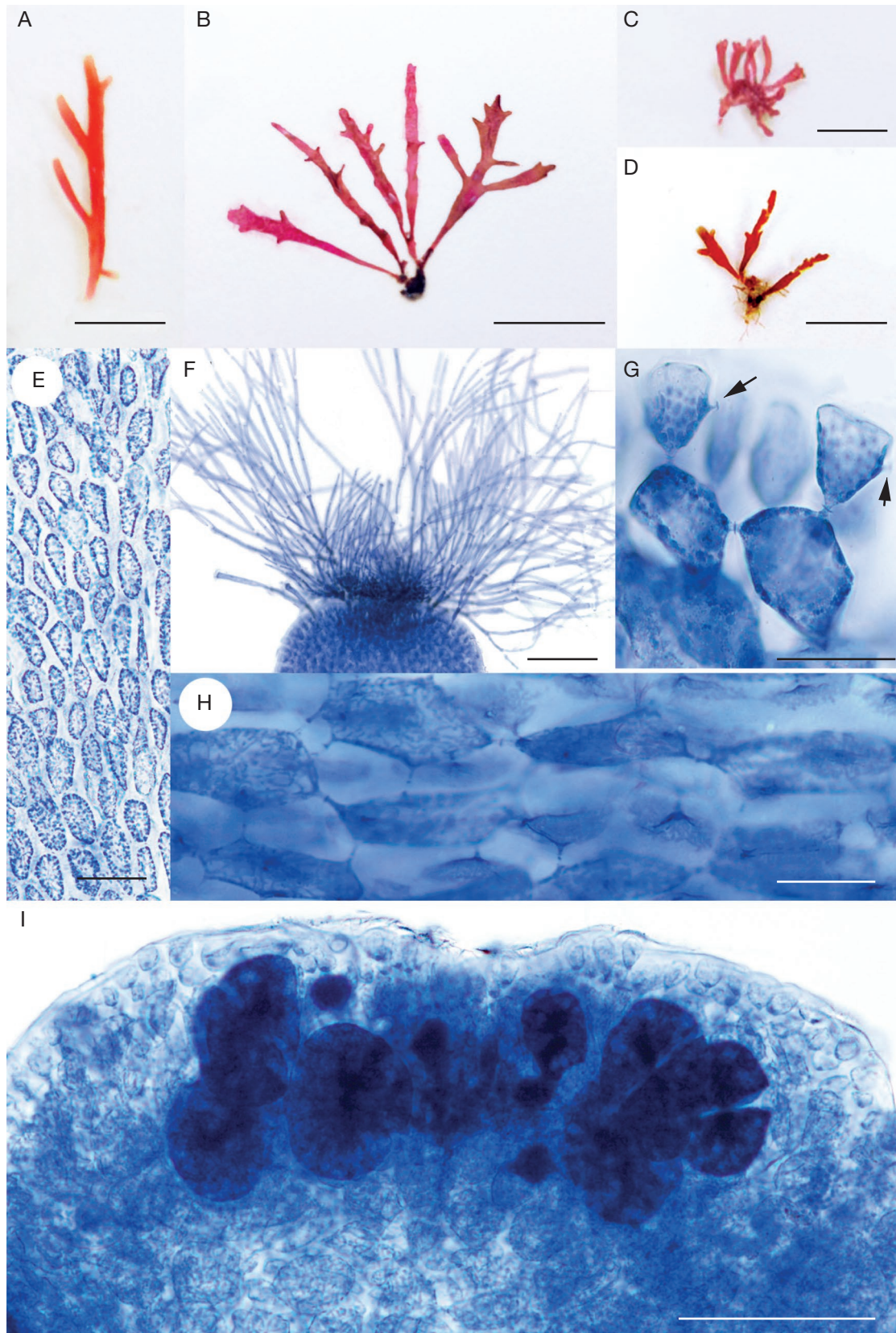


FIG. 5. — *Chondrophyucus planiparvus* Popolizio, C.W.Schneider & C.E.Lane sp. nov. **A**, holotype specimen [TRP 12-40-13/BDA0934]; **B**, specimen with two branched axes arising from a common holdfast [CWS/CEL 9-30-9]; **C**, habit of small live specimen, [TRP 12-160-8/BDA1741]; **D**, habit of small pressed specimen [TRP 12-148-6/BDA1625]; **E**, axial view of cortex showing irregularly angular to ovoid surface cells [TRP 12-148-6/BDA1626]; **F**, branch apex with new and mature trichoblasts emerging from an apical pit [CWS/CEL 9-30-9]; **G**, secondary pit connections (arrowheads) between adjacent outer cortical cells in transverse section [TRP 12-40-13/BDA0934]; **H**, whole mount surface view of outer cortex in lower portions of axes showing irregularly angled surface cells and secondary pit connections [CWS/CEL 09-30-9]; **I**, longitudinal section of branch tip showing right-angle arrangement of tetrasporangia [TRP 12-160-8/BDA1741]. Scale bars: A, C, 5 mm; B, D, 1 cm; E, H, 50 μ m; F, 200 μ m; G, 40 μ m; I, 100 μ m.

material collected at Heron Bay, Bermuda (*P.B.-A.* no. 1937, as *Laurencia tuberculosa* J.Agardh; Collins *et al.* 1913). The *P.B.-A.* exsiccata has specimens of this number representing at least two heterotypic members of the ‘*Laurencia-complex*’. Early workers moved all *P.B.-A.* no. 1937 material to *Laurencia poiteaui*, yet one representative specimen (MICH 6605) is *L. intricata*, while the other (MICH 622078) is likely *Yuzurua poiteaui*.

The first account of *Laurencia microcladia* in the literature is by Kützing (1865: 22, pl. 60, figs b, c) who illustrated material from the West Indies in a way that distinctly highlights the virgate habit of this species. Børgesen (1915) later reported *L. obtusa* var. *gelatinosa* (Desfontaines) J.Agardh from the region, a name that has since been placed in synonymy with *L. microcladia*. Collins & Hervey (1917) described their collections (reported as *L. obtusa* var. *gelatinosa*) as a “low and slender form of exposed rocky shores” archetypal of this species. Howe (1918) also notes that intertidal collections of *L. microcladia* from Bermuda are included as “*P.B.-A.* no. 1888, as *L. obtusa* var. *gelatinosa*” (Collins *et al.* 1912). In his account, Børgesen (1915) highlights the pyramidal shape of the thallus, nature of verticillate branching with swollen, clavate branchlets (Fig. 2A), and the tendency of this species to exist in particularly exposed habitats. His illustration of the U.S. Virgin Islands specimen bears a remarkable resemblance to our *L. microcladia* from St. Croix, USVI (Fig. 2B). Taylor (1960) provided the first detailed description of *L. microcladia* for the western Atlantic which fits observations of our specimens from both Bermuda and St. Croix with morphological overlap in all characters for which data have been reported by various authors since (Table 3).

Intraspecific divergence values for specimens assigned to *Laurencia microcladia* are 0.5% and 0.4% for COI-5P and *rbcL*, respectively, compared with interspecific divergences of 4.6% and 1.2%. To further support the conspecificity of *L. microcladia* specimens we collected at the Caribbean type locality with those from Bermuda, we compared ITS intraspecific sequence divergences for several isolates of *L. microcladia* and two additional species (*L. catarinensis* and *L. dendroidea*) within *Laurencia* (Appendix 2), as well as distances to nearest neighbor, as reported in the results section above. We found that intraspecific divergence for *L. microcladia* was a maximum of 2.1% while the distance to the nearest neighbor species (*L. dendroidea*) was 29.2% (Table 2). Based on these values, as well as the analyses described above, we consider that specimens of *L. microcladia* from Bermuda and St. Croix represent a single taxon.

Surprisingly, *Laurencia microcladia*, a fairly common intertidal species in Bermuda and the Caribbean Antilles (Taylor 1960), has not been included in any molecular studies of the *Laurencia* complex that have been conducted over the past several years in Mexico or Brazil (e.g., Martin-Lescanne *et al.* 2010; Fujii *et al.* 2011; Senties *et al.* 2011, 2019; Casano *et al.* 2012a, 2012b, 2019; Machín-Sánchez *et al.* 2012; Machín-Sánchez *et al.* 2018; Mateo-Cid *et al.* 2014). Fujii & Senties (2005) document previous reports of *L. microcladia* in Brazil (Oliveira Filho 1977; Cordeiro-Marino 1978;

Pinheiro-Joventino *et al.* 1998; Figueiredo *et al.* 2004) but do not include the species in their detailed monograph of the complex in Brazil. The authors do, however, include *L. venusta* Yamada, a species from Japan reported for the first time in the Atlantic by Senties *et al.* (2001) from the Mexican Caribbean, and described to be “entirely in concordance” with Japanese material examined by Saito (1964) and without “significant differences” from Yamada’s (1931) type specimen. The authors briefly mention the similarities between Mexican *L. venusta* and *L. chondrioides* Børgesen from the West Indies but do not discuss similarities with other western Atlantic species of the genus, including *L. microcladia*, with which it shares a significant number of morphological characteristics (Table 3). The features of *L. microcladia* from the western Atlantic, including Bermuda, conform to all of the vegetative and reproductive characters described for *L. venusta* from this region, except that in *L. venusta*, sparse verticillate branching is emphasized. *Laurencia microcladia* is densely branched and possesses verrucose branchlets that are clustered in a manner that creates a whorled appearance, however, branching overall is more irregular than verticillate (Fig. 3A). Additionally, though the observed diameters for tetrasporangia and cystocarps in the two species overlap, the upper limits of these tend to be larger in *L. microcladia* than in *L. venusta*, especially compared with Caribbean specimens of the latter species (Table 3).

Our *rbcL* sequences from specimens of *Laurencia microcladia* are almost identical to those from a specimen identified as *L. venusta* from Caribbean Mexico, with only 0.2–0.4% divergences between the sequences. Specifically, two of 1217 base pairs were different between our St. Croix specimen and the GenBank data for *L. venusta* from Caribbean Mexico; five differences were present between both Caribbean specimens and Bermuda specimens. It is likely that the entities shown in the previous analyses are genetic variants of *L. microcladia*, a name that precedes *L. venusta* by more than half a century. Alternatively, the two may represent cryptic species from different ocean basins, but given the near genetic equivalence of these specimens as clearly demonstrated by our data, we think that this is doubtful. While molecular sequence data of *L. venusta* from Australia are clearly distinct in this analysis, data from *L. venusta* from the type locality in Japan will be required to decisively clarify this matter.

Our specimens of *Laurencia microcladia* are also closely related in *rbcL* sequence analysis to *L. laurahuertana* Mateo-Cid, Mendoza-Gonzalez, Senties & Díaz-Larrea (Mateo-Cid *et al.* 2014) with 0.5% sequence variation. As such, the vegetative and reproductive characteristics observed in this species are presented for comparative purposes in Table 3. *Laurencia laurahuertana* is distinguished from *L. microcladia* by its unusually diminutive size and exclusively being an epiphyte of seagrasses. *Laurencia microcladia* specimens collected in Bermuda are strictly intertidal and epilithic with the exception of two shallow subtidal specimens from Spanish Point and Shelly Bay, but tidal exposure at these locations is possible during the lunar cycle. The presence of fertile specimens of *L. laurahuertana* suggests that these are not simply immature

stages in the life cycle of a larger species. Other notable differences in *L. laurahuertana* include cortical cell projections (absent in *L. microcladia*), markedly smaller tetraporangial, cystocarpic and carposporangial diameters, and the absence of a sterile apical cell in spermatangial stichidia. Genetic variation between and *L. laurahuertana* and Bermuda *L. microcladia* is well within the intraspecific limits defined for the genus; however, it should be noted that the *rbcL* sequence of *L. laurahuertana* available in GenBank is shorter in sequence length (826 bp) than those that we produced (1217 bp). Thus, longer *rbcL* sequences from *L. laurahuertana* are needed to know definitively whether it is synonymous with *L. microcladia*.

Another *rbcL* sequence, from a specimen identified as *L. caduciramulosa* from Key Biscayne, Florida, is closely aligned to our *L. microcladia* sequences, with 0.5% intraspecific divergence. But when compared with sequences from specimens identified as *L. caduciramulosa* from Spain and Brazil, the Florida species differs by 1.2%. Since molecular data group this species more closely with our *L. microcladia* than *L. caduciramulosa*, we compared morphology for the two, along with those of *L. caduciramulosa* from Vietnam, the type locality (Table 3), but morphological features largely overlap for the two species where data are available to assess. Reproductive characters are not reported for *L. caduciramulosa* from either location, making diagnosis based on morphology impracticable. For now, the molecular data suggest that the species from Florida is indeed *L. microcladia*, and not *L. caduciramulosa* from the Pacific.

THE GENUS *PALISADA* IN BERMUDA

The molecular sequence data we have produced verify that *Palisada perforata* in Bermuda is conspecific with specimens from the type locality (Canary Islands, Spain) with 0.6% and 0.2% intraspecific divergence in COI-5P and *rbcL*, respectively. This species is the most common member of the genus *Palisada* in our *Laurencia* complex collections, and is predominantly intertidal with a few exceptions from shallow subtidal sites in the Florida Keys and a single subtidal collection from a shallow subtidal site (3–4 m) off Bermuda's north shore. Another species in the genus, *P. flagellifera*, with a type locality in the Indian Ocean, is reported as pantropical with amphiatlantic reports from Cuba (Areces *et al.* 2003), Brazil (Fujii *et al.* 2006) and the Canary Islands (Gil-Rodríguez *et al.* 2010). Our COI-5P barcode investigation indicated a group within the *Palisada* clade that was distinct from reported Bermuda species – *rbcL* sequences from these collections align with *P. flagellifera* sequences from Brazil and the Canary Islands (intraspecific divergence = 0.2%). Comparative molecular data are not available for specimens from the Indian Ocean type locality. The present report represents the first record of *P. flagellifera* in Bermuda.

Accounts of *Palisada corallopsis* (as *Laurencia corallopsis*) (Montagne) M. Howe in Bermuda (type locality = Cuba) have appeared in the literature since the early 20th century [Howe 1918, as *L. corallopsis*; Frederick 1963, as *L. corallopsis*; Schneider 2003, as *Chondrophyucus corallopsis* (Montagne) K.W.Nam]. Harvey's (1853) *L. cervicornis* Harvey (type locality

= Key West) had long been merged with *P. corallopsis* (Howe 1918) and Collins *et al.* (1917, *P.B.-A.* no. 2187) and Collins & Hervey (1917) reported their collections from Bermuda as *L. cervicornis* Harvey (Schneider 2003). Littler & Littler (2000: 490, as *L. cervicornis*) argued that *P. cervicornis* was smaller in habit with smaller surface cells than *P. corallopsis* and therefore distinct from the latter, a position accepted by Dawes & Mathieson (2008). More recently, specimens of *P. cervicornis* and *P. corallopsis* collected from the Florida Keys were included in a phylogenetic analysis that supported these species as unique (Collado-Vides *et al.* 2017).

Specimens field-identified as *Palisada corallopsis* from Bermuda and the Florida Keys are genetically variable in both COI-5P and *rbcL* analyses. For the latter gene, one genetic entity from Bermuda is closely related (0.6% divergence) to a specimen from Caribbean Mexico likewise identified as *P. corallopsis*, and considered to be representative of the species due to its proximity to the type locality (Cuba). Collado-Vides *et al.* (2017) published an *rbcL* sequence of *P. corallopsis* from material collected in Florida that differed by 0.4% from the Caribbean Mexico specimen sequence, similar to the genetic divergence seen between the latter and Bermuda specimens. The other genetic entity from Bermuda previously identified as *P. corallopsis* aligns instead with specimens of *P. cervicornis* also reported by Collado-Vides *et al.* (2017) with 0.9% divergence in *rbcL* between the sequences. A third undescribed species that we collected in the Florida Keys is sister to *P. cervicornis* from Bermuda and Florida (2.0% divergence in *rbcL*, Table 1).

Our collections grouping with Caribbean specimens identified as *Palisada corallopsis* cannot be distinguished from Montagne's (1842) protologue of *Sphaerococcus corallopsis* Montagne (now *P. corallopsis*) from Havana, Cuba. Our specimens grouping with *L. cervicornis* from Florida are morphologically indistinguishable from the Collins *et al.* (1917) Bermuda specimens in *P.B.-A.* (no. 2187), except for the presence of uniform medullary cell wall thickenings in the recently collected Bermuda specimens. These were not found when examining Collins' specimens. However, both are in accordance with the original description of *L. cervicornis* provided by Harvey (1853). Without genetic sequencing, we have opted to leave *P.B.-A.* (no. 2187) under this name as Harvey called it, with the assumption that cell wall thickening is a variable trait.

The absence of lenticular thickenings is also observed when comparing recent Bermuda collections of *Palisada cervicornis* and *P. corallopsis*, the latter species lacking this character. *Palisada cervicornis* specimens from Bermuda have thinner main axes, though this may simply be a result of younger age. In Bermuda specimens, surface cell diameters are also marginally smaller in *P. cervicornis* (18–30 µm) compared to *P. corallopsis* (23–45 µm), in line with the observations for Caribbean isolates (Littler & Littler 2000). Other *Palisada* specimens in this clade collected in Key West are morphologically distinct from the two Bermuda species as well as *P. cervicornis* specimens described by Collado-Vides *et al.* (2017) from Florida (Table 4). Further study is required to determine whether

TABLE 4. — Morphological character comparisons for treatments of *Palisada cervicornis* (Harvey) Collado-Vides, Cassano & M.T.Fujii, *P. corallopsis* (Montagne) Senties, M.T.Fujii & Díaz-Larrea and *P. furcata* (Cordeiro-Marino & M.T.Fujii) Cassano & M.T.Fujii.

| | <i>Sphaerococcus corallopsis</i> (protologue) | <i>Palisada corallopsis</i> | <i>Palisada cervicornis</i> | <i>Palisada cervicornis</i> | <i>Laurencia cervicornis</i> (protologue) | <i>Palisada furcata</i> |
|--|--|--|---|---|---|---|
| Location of specimens used for data | Havana, Cuba (type locality) | Bermuda | Bermuda | Florida Keys – cultured in vitro | Key West, Florida (type locality) | Brazil (type locality) |
| Length of upright axes (cm) | – | to 8 | to 2 | 5-6 (<1 in field) | to 4 | to 15 |
| Main axis basal diam. (mm) | – | 1.5-2.0 | 0.5-1.0 | – | – | 1.3-1.5 |
| Branching pattern | Irregularly dichotomous or whorled; dichotomous above with short nearly dichotomous branchlets solitary or in clusters | Irregularly cervicorn; apices often appearing dichotomous; some adventitious branching | Irregularly palmate; branches varying in width/length at each node; to 10 branches per node | Scarcely branched, irregular to dichotomous usually with 1-2 orders of branches | Irregularly branched to subdichotomous; secondary branches curved upwards | Dichotomously, trichotomously to irregularly branched, more densely in upper portions |
| Branchlet diam. (mm) | 1-2 | 1-2 | to 1.5 | 0.7-1.2 | to 2 | 1.0-1.5 |
| Branchlet tips | Slightly swollen with apical pit; trichoblasts present | Swollen; broad in proportion to length; trichoblasts present | Slightly swollen; trichoblasts present | – | Cylindrical; broad in proportion to length; trichoblasts present | Cylindrical to slightly flattened; tips obtuse |
| Secondary pit-connections | – | Present | Present | Present | – | Present |
| Medullary cells | – | – | – | Rounded or slightly radially elongated; 51-101 long, 30-83 wide | – | Slightly rounded; 50-150 long, 45-135 wide |
| Lenticular thickenings | – | Absent | Uniform cell wall thickening present | Absent (but medullary cell walls uniformly thickened) | – | – |
| Corps en cerise | – | – | – | – | – | Absent |
| Outer cortex cell in surface view | – | Polygonal (hexagonal-rectangular) | Polygonal (hexagonal) | Polygonal and isodiametric | – | Polygonal and isodiametric |
| Outer cortex cell diam. (µm), surface view | – | 23-45 | 18-30 | 16-34 (22-48 long) | – | 7-33 (21-33 long) |
| Outer cortex cell projections | – | Absent | Absent | – | – | Absent |
| Tetrasporangium diam. (µm) | – | – | – | 38-91 | – | 60-75 |
| References | Montagne 1842 | Present study | Present study | Collado-Vides <i>et al.</i> 2017 | Harvey 1853 | Fujii & Senties 2005 |

the Key West collections represent a known or novel species of *Palisada*.

Palisada furcata from Brazil also groups in the *P. corallopsis* clade, with 1.8% divergence from its closest congener, *P. corallopsis* from Mexico. But there are 14 ambiguities in the *P. furcata* sequence, so that distance estimate is likely to change with better quality sequence data. While the phylogenetic relationship of *P. furcata* to *P. corallopsis* is unresolved in our analysis (Fig. 1), the close grouping warrants comparing the morphological characters for these species (Table 4). *Palisada furcata* can be distinguished from *P. corallopsis* morphologically by its larger overall habit, cylindrical to slightly flattened (vs. swollen) branchlet tips, and smaller outer cortical cells.

Unfortunately, we did not collect fertile *P. corallopsis* to compare tetrasporangia, a character that has not been described for this species in previous publications.

THE GENUS *YUZURUA* IN BERMUDA

Reports of the species currently known as *Yuzurua poiteaui* appear in the earliest literature for Bermuda as *Laurencia gemmifera* Harvey (Rein 1873; Dickie 1874; Hemsley 1884). This species was archived *pro parte* as *P.B.-A.* no. 1937 (as *L. tuberculosa*; Collins *et al.* 1913), and as mentioned above, represents *Y. poiteaui* in a heterotypic collection; however a specimen of the same *P.B.-A.* number in another fascicle can be attributed to *L. intricata*. Collins & Hervey (1917)

first reported the species in Bermuda as *Laurencia poiteaui* (J.V.Lamouroux) M.Howe. This name was later transferred to *Chondrophyucus* (Nam 1999) and then to *Palisada* (Nam 2006, 2007) based on phylogenetic and morphological evidence. Using the *rbcL* sequences of *Y. poiteaui* (as *Chondrophyucus poiteaui* (J.V.Lamouroux) K.W.Nam) and *C. gemmiferus* (Harvey) Garbary & J.T.Harper, Díaz-Larrea *et al.* (2007) concluded that the latter species, different only in minor anatomical characters and should be reduced to a synonym of *Palisada poiteaui* (J.V.Lamouroux) K.W.Nam (Senties & Díaz-Larrea 2008). Molecular data have also prompted the elevation of *Yuzurua*, initially a subgenus of *Chondrophyucus* recognized by Nam (1999), to the generic level (Martin-Lescanne *et al.* 2010) with *Y. poiteaui* as the generitype. This species appears to be relatively rare in Bermuda at present, with only one collection confirmed with molecular data (intraspecific divergence of 0.2% in *rbcL*). *Yuzurua poiteaui* specimens were far more abundant in our Florida Keys and US Virgin Islands collections.

Sequence data have shown that *Palisada iridescens* (M.J.Wynne & D.L.Ballantine) K.W.Nam was closely related to *Yuzurua*, and the new combination, *Y. iridescens* was proposed (Senties *et al.* 2015). Our data agree with this transfer, as previous records of this species in Bermuda (Schneider & Lane 2007, as *Chondrophyucus iridescens*) grouped with the *Yuzurua* clade in both our COI-5P and *rbcL* barcode analyses (Table 1) and *rbcL* phylogeny (Fig. 1). While sequence data for *Y. iridescens* from Guadeloupe, Mexico and St. Kitts are available in GenBank, we chose to exclude these data from our analysis. The sequences of *Y. iridescens* from St. Kitts and Guadeloupe were short (886 bp and 660 bp, respectively) and only overlapped by 173 bp with our *rbcL* sequences, an inadequate number for meaningful comparison. Furthermore, the three sequences of *Y. iridescens* from Senties *et al.* (2015) deposited in GenBank are quite variable, despite their stating that the divergence among them was extremely low at 0.01–0.02%. Our analysis shows much larger distance values of 1.4–5.5%. It is clear that the *L. iridescens* complex needs reassessment so these issues can be resolved. Additional genes and longer sequences from specimens at or near the type locality will be imperative for definitive phylogenetic results.

Our analysis has also resolved a unique sequence from a Bermuda specimen in this clade sister to *Yuzurua poiteaui* (4.3% divergence). Thus far, we are able to confirm only a single specimen representing this entity and will require additional collections before we can verify that these represent a unique third species in the genus. At present, this taxon will be regarded as *Yuzurua* sp. 1Bda (Fig. 1; Appendix 1).

THE GENUS *LAURENCIELLA* IN BERMUDA

The genus *Laurenciella* was segregated from *Laurencia* (Cassano *et al.* 2012b) on the basis of molecular sequence data, which showed it to be a distinct clade despite its generic features being indistinguishable from those of *Laurencia*. The type of the genus, *Laurenciella marilzae* (Gil-Rodríguez, Senties, Díaz-Larrea, Cassano & M.T.Fujii) Gil-Rodríguez, Senties, Díaz-Larrea, Cassano & M.T.Fujii, was originally described from the Canary

Islands (Gil-Rodríguez *et al.* 2009, as *Laurencia marilzae* Gil-Rodríguez, Senties, Díaz-Larrea, Cassano & M.T.Fujii) based on *rbcL* sequences and characterized morphologically by the distinctive yellow-orange color of its habit (Fig. 4A), cortical cells that project markedly in cross-section, and the presence of ‘*corps en cerise*’ in all cells of the thallus. Corroborating evidence from both molecular and morphological analyses of specimens collected in the Mexican Caribbean showed that this species was also present in the tropical western Atlantic Ocean (Senties *et al.* 2011). More recently, a second species from the genus, *L. mayaimii* Collado-Vides, Cassano & M.T.Fujii, was described from Florida (Collado-Vides *et al.* 2018).

Our molecular findings show a clear relationship between *Laurenciella marilzae* and specimens that we collected in Bermuda and the Florida Keys. Both genetic variation (3.9% divergence in *rbcL*) and differences in overall habit morphology suggested that these latter collections were a distinct second species of the genus, described herein as *L. namii* Popolizio, C.W.Schneider & C.E.Lane, sp. nov. Not excepting the shared features of *Laurenciella* and *Laurencia sensu stricto* (i.e., four pericentral cells in axial segments; presence of ‘*corps en cerise*’; presence of secondary pit connections), microscopic vegetative characters of *L. marilzae* and *L. namii* sp. nov. predominantly overlap (Table 5). In particular, the size and shape of outer cortical cells (Fig. 4D, F), the size and shape of medullary cells (Fig. 4E), the conspicuous projecting of cortical cells in cross-section (Fig. 4D) and the presence of trichoblasts with 3–4 orders of subdichotomous branching all represent shared characteristics (Fig. 4F, G). In addition, Bermuda and the Florida Keys specimens of *L. namii* sp. nov. are distinctly yellow-orange in color (Fig. 4A, B), an identifying feature that is noted for specimens of *L. marilzae* from the type locality and from the Caribbean Sea. However, this does not appear to be a characteristic of the genus as a whole because deep-occurring Brazilian specimens (Rocha-Jorge *et al.* 2010), as well as an undescribed genetic isolate (*Laurenciella* sp. 1Bda; Fig. 1), are markedly red in color.

Though the vegetative anatomy appears to be largely cryptic between *Laurenciella marilzae* and *L. namii* sp. nov., the two species are quite distinct in overall habit. *Laurenciella namii* sp. nov. reaches twice the height of *L. marilzae* and has a thallus texture that is fleshy rather than cartilaginous. The main axes of *L. namii* sp. nov. are slender and are distinctly lax (Fig. 4A), never displaying the characteristic “turf” form possessed by *L. marilzae* in the Caribbean (Senties *et al.* 2011). Branching patterns in *L. namii* sp. nov. are more irregular than alternate (Fig. 4A, B), with upper portions of the thallus tending to be profusely branched, whereas lower portions are often denuded at maturity (Fig. 4A). The habitats of both Caribbean and Canary Islands specimens of *L. marilzae* are documented as exposed sites in the low intertidal zone (Gil-Rodríguez *et al.* 2009, Senties *et al.* 2011). Our collections of *L. namii* sp. nov. from Bermuda and Florida are exclusively found in the subtidal and are especially common in shallow, relatively protected habitats at both locations.

Therefore, after a thorough assessment of species in the ‘*Laurencia*-complex’ from the western Atlantic, we deter-

TABLE 5. — Morphological character comparisons of the species of *Laurenciella* Cassano, Gil-Rodríguez, Senties, Díaz-Larrea, M.C.Oliveira & M.T.Fujii.

| | <i>Laurenciella marilzae</i> | <i>Laurenciella mayaimii</i> | <i>Laurenciella namii</i> sp. nov. |
|--|--|---|---|
| Thallus color | main axes yellow-orange, ultimate branches rosy red | main axes brownish-yellow, ultimate branches rosy red | main axes yellow to orange, ultimate branches deep rosy red |
| Length of upright axes (cm) | to 7 | to 6 | to 15 |
| Main axis basal diam. (mm) | to 1.5 | to 0.9 | to 1 |
| Branching pattern | irregularly alternate and spiral | subopposite to spirally alternate | subopposite to spirally alternate |
| Branchlet diam. (µm) | 540-820 | 410-430 | 140-350 |
| Secondary pit-connections | present | present | present |
| Corps en cerise | present, one per cortical cell | present, one per cortical cell | present, one per cortical cell |
| Outer cortex cell in surface view | isodiametric-polygonal above, elongate-polygonal below | isodiametric-polygonal | irregularly rounded polygonal to ovoid above, elongate-polygonal below |
| Outer cortex cell diam. in surface view (µm) | 28-53 | 20-89 | 20-49 |
| Outer cortex cell projections | present | present | present |
| Medullary cells diam. (µm) | 10-100 | – | 30-115 |
| Known distribution | Canary Is., Azores, Mediterranean Sea, Brazil, Mexico | Florida | Bermuda, Florida |
| References | Gil-Rodríguez <i>et al.</i> 2009 (as <i>Laurencia marilzae</i>) | Collado-Vides <i>et al.</i> 2018 | Present study; Collado-Vides <i>et al.</i> 2018, as <i>L.</i> sp. Florida |

mined that our specimens of *Laurenciella namii* sp. nov. are unique. We did consider the historical name *Laurencia obtusa* var. *gracilis* (C.Agardh) Kützing based on the illustrations and description of Kützing (1865), which we interpreted as “delicate branches spreading widely,” and of Collins & Hervey (1917) who describe it as a “delicate, soft and slender form.” Without seeing the original *Chondria obtusa* var. *gracilis* in Lund that Agardh (1822) reported from the West Indies, we believe linking this variety to the new species of *Laurenciella* would be unwise at present. We did not observe *Laurencia obtusa* var. *gracilis* in our collections from St. Croix in the West Indies, the type locality of this variety. Interestingly, images of specimens from Bermuda with the characteristics of *Laurenciella namii* sp. nov., also previously identified as *Laurencia obtusa*, can be found illustrated on the Macroalgal Herbarium Portal (<https://macroalgae.org/portal/collections/index.php>), so this large species in the complex has been an important member of the flora as long as specimens have been collected in the islands.

A second genetically distinct species of *Laurenciella* from Bermuda has been discovered in this study. Based on *rbcL* sequences, the closest neighbor to ‘*Laurenciella* sp. 1Bda’ (Fig. 1) is an undescribed specimen from Brazil, *Laurenciella* sp. 2 (Cassano *et al.* 2012b) from which it differs by 0.4%. These likely represent a single species of *Laurenciella* with a broad distribution in the western Atlantic. A second undescribed species from Brazil, *Laurenciella* sp. 3 (Cassano *et al.* 2012b) is closely related to these, with 0.9% divergence in *rbcL*. As with *Yuzurua* sp. 1Bda, we have confirmed only a single collection representing this taxon.

THE GENUS *CHONDROPHYCUS* IN BERMUDA

Our COI-5P and *rbcL* barcode analyses (Table 1) uncovered a unique taxon in the genus *Chondrophyucus* from Bermuda, herein described as *C. planiparvus* Popolizio, C.W.Schneider & C.E.Lane, sp. nov. Sequences from *Chondrophyucus* cf. *undulatus* (Yamada) Garbary & J.T.Harper and *C. dotyi* (Y.Saito)

K.W.Nam collected in the Hawaiian Islands, grouped with our new Bermuda species in COI-5P barcode gap analysis (Table 1). In the *rbcL* analysis, *C. planiparvus* sp. nov. differs by only 0.5% from an undescribed specimen collected from Flower Garden Banks, Gulf of Mexico (Fujii *et al.* 2006) (Table 1 and Fig. 1), and these may represent the same species. The two taxa are arranged as a sister grouping to the rest of the *Chondrophyucus* clade, which consists of *C. dotyi* from Hawaii, *C. anabeliae* Senties, M.T.Fujii, Cassano & Dreckmann from Caribbean Mexico, *C. tronoii* (E.Ganzon-Forbes) K.W.Nam from the Philippines, *C. cf. undulatus* from New Caledonia and several undescribed species from South Africa, Australia or New Caledonia. The recently described *C. anabeliae* from the Caribbean (Senties *et al.* 2016) has terete axes, but these are occasionally partially compressed. It bears little morphological resemblance to *C. planiparvus* sp. nov.

Saito (1967) split the genus *Laurencia* into two subgenera, *Laurencia* and *Chondrophyucus*, on the basis of tetrasporangial development relative to the axis (parallel or right-angle) and presence or absence of secondary pit connections between cortical cells. He later determined these features were unreliable since some species possessed features of both subgenera, namely, a parallel arrangement of tetrasporangia and lack of secondary pit-connections (Saito 1982). Species exhibiting this combination of characters would later be attributed to *Osmundea* (Nam *et al.* 1994). Ultimately, Garbary & Harper (1998) elevated the subgenus *Chondrophyucus* to generic rank based on morphological cladistics, including the absence of secondary pit connections.

Nam (1999) proposed an infrageneric classification scheme for *Chondrophyucus* including four subgenera – *Chondrophyucus*, *Kangjaewonia*, *Palisada* and *Yuzurua*. Members of the subgenus *Chondrophyucus* (containing *C. cartilagineus* (Yamada) Garbary & J.T.Harper as the type, as well as several others) exhibit right-angle development of tetrasporangia but lack secondary pit connections. For species displaying both

TABLE 6. — Morphological character and habitat comparisons for species of *Chondrophyucus* (J.Tokida & Y.Saito) Garbary & J.T.Harper with compressed axes.

| | <i>C. dotyi</i> | <i>C. kangjaewonii</i> | <i>C. planiparvus</i> sp. nov. | <i>C. succisus</i> | <i>C. undulatus</i> |
|---------------------------------|--|--|--|--|--|
| Type locality | Hawaii | Korea | Bermuda | Australia | Japan |
| Length of upright axes | to 5 cm (subcompressed) | to 10 cm (compressed) | to 2 cm (compressed) | to 8 cm (compressed) | to 7 cm (compressed) |
| Branching pattern | Distichous; alternate, opposite or irregular | Distichous; alternate | Distichous; irregular to alternate or opposite | Distichous; opposite (pinnate) or alternate | Distichous; opposite (pinnate) |
| Secondary pit connections | Absent | Absent | Present (abundant, conspicuous) | Absent | Absent |
| Outer cortex cells surface view | Nearly isodiametric | Elongated ovoid | Ovoid in upper regions of branches, irregularly angular and elongated below | Rounded polygonal to longitudinally elongate | Quadrangular |
| Outer cortex cell projection | Domed projections present in ultimate branchlets | Absent or occasionally slightly projecting at branch apices | Cortical cell projections present at most branch apices | Absent | Absent |
| Tetrasporangial arrangement | Right-angle | Parallel | Right-angle | Right-angle | Right-angle |
| Tetrasporangia diam. (µm) | Not reported | 180–230 | 43–68 | Not reported | to 110 |
| Habitat | Intertidal; on eroded coral and basalt platforms | Lower intertidal on rock or coral or subtidal to 3 m | From 13–23 m on coral; never intertidal | Intertidal; on eroded coral and basalt pools | Lower intertidal, more commonly on basalt rock |
| References | Saito 1969; Abbott 1999 | Nam & Sohn 1994, Nam 1999 | Present study | Cribb 1958; Saito 1969; Abbott 1999 | Yamada 1931; Tseng 1943; Nam 1999; Abbott 1999 |

right-angle arrangement of tetrasporangia and secondary pit connections, Nam (1999) circumscribed the subgenus *Yuzurua*, which has since been elevated to generic status and is unquestionably distinct from *Chondrophyucus* in phylogenetic analyses (Martin-Lescanne *et al.* 2010). Furthermore, Nam (1999) defined the section Parvipapillatae for members of subgenus *Yuzurua* demonstrating epidermal cell projections at branchlet apices in transverse section, and designated *C. parvipapillatus* (C.K.Tseng) Garbary & J.T.Harper as the type species of this section. Later, Nam (2006) proposed the genus *Palisada* following a morphological cladistics analysis that resolved two paraphyletic clades of *Chondrophyucus* species. *Chondrophyucus parvipapillatus* fell into the clade that did not include *C. cartilagineus*, the generitype, and thus was transferred to *Palisada*.

Interestingly, our specimens of *Chondrophyucus planiparvus* Popolizio, C.W.Schneider & C.E.Lane, sp. nov. from Bermuda exhibit the three traits that Nam (2006) used to segregate *Palisada parvipapillata* (C.K.Tseng) K.W.Nam to *Palisada*: a right-angle arrangement of tetrasporangia, production of secondary pit connections and apical cortical cell projections. Secondary pit connections are noted to be sporadic in *P. parvipapillata*, but are frequent and conspicuous in *C. planiparvus* sp. nov., and in the former species, cortical cell projections are present throughout the thallus, whereas these are only occasionally seen in the latter, strictly at branch apices. In our analyses, COI-5P sequence data from a Hawaiian specimen of *P. parvipapillata* place the species within the genus *Palisada* (Table 1), providing molecular evidence for its correct position in the genus and dismissing it as a possible range extension from Bermuda species, despite some morphological similarities.

Table 6 delineates the morphological differences *Chondrophyucus planiparvus* Popolizio, C.W.Schneider & C.E.Lane, sp. nov. has with congeners having compressed or flattened axes. Our Bermuda species is distinguished from these in having upright axes 2 cm long or smaller (Fig. 5A–D) and by the conspicuous secondary pit connections present between cortical cells (Fig. 5D, H), a character that historically has been used to segregate morphological subclades of taxa. *Chondrophyucus planiparvus* sp. nov. represents the only current species of the genus that possesses secondary pit connections. However, this trait is not synapomorphic in other genera in the *Laurencia* complex, including its sister genus *Osmundea*. McIvor *et al.* (2002) suggested that secondary pit connections may be an ancestral state that was subsequently lost in some lineages or species in the complex, a concept that is not easily rationalized given our poor knowledge of pit connection functionality on the whole. Nevertheless, the presence of this character in the Bermuda specimens provides an interesting contrast to other members of the genus. Of the species of *Chondrophyucus* exhibiting compressed axes, only *C. kangjaewonii* (K.W.Nam & C.H.Sohn) Garbary & J.T.Harper lacks sequence data available from GenBank, but this species is easily distinguished from *C. planiparvus* sp. nov. by its parallel arrangement of tetrasporangia, which are also three or four times larger.

Notably, all of the compressed species of the genus from the Pacific Ocean are found in intertidal habitats (or shallow subtidal, as in *C. kangjaewonii*). *Chondrophyucus planiparvus* Popolizio, C.W.Schneider & C.E.Lane, sp. nov. specimens have been collected exclusively in subtidal waters off the south shore of Bermuda, from depths of 13–23 m during December–March, when water temperatures in Bermuda are at their lowest. These findings suggest that this novel species

is adapted to cooler water temperatures and lower light levels than its most similar congeners.

CONCLUSIONS

Along with the two new species from Bermuda, *Laurenciella namii* Popolizio, C.W.Schneider & C.E.Lane, sp. nov. and *Chondrophyucus planiparvus* Popolizio, C.W.Schneider & C.E.Lane, sp. nov., we distinguish the formerly synonymized *Palisada cervicornis* from *P. corallopsis* in Bermuda, present the first report of the Indo-Pacific species *P. flagellifera* in the islands, and provide the first detailed description of *Laurencia microcladia* from the type locality (Caribbean Sea). Further, two genetic species that have historically been identified as *L. obtusa* in Bermuda are shown to be distinct from isolates of that taxon from near its type locality (England). These have been determined to be *L. dendroidea* and *L. catarinensis*, both with type localities in Brazil. Therefore, *L. obtusa* is removed from the Bermuda flora.

Much of the recent research effort on the *Laurencia* complex has been focused on *rbcL* gene sequencing. While this has resulted in rich comparative data that are useful for assigning specimens to species as well as genera, *rbcL* has not been shown to be an effective marker for resolving relationships at the deeper nodes of the phylogeny in this group. The unsupported intergeneric relationships described above in the molecular results section demonstrate the need for further research that integrates additional taxa (including archival type specimens or recent topotype specimens) and genes with rigorous phylogenetic analyses to produce a bona fide evolutionary framework for the *Laurencia* complex.

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REFERENCES

- ABBOTT I. A. 1999. — *Marine Red Algae of the Hawaiian Islands*. Bishop Museum Press, Honolulu, 477 p.
- AGARDH C. A. 1822. — *Species algarum...* Vol. 1(2). Lundae [Lund]: 169-398.
- ARECES J. A., SENTIES A. & ZAYAS C. R. 2003. — Nuevas adiciones al género *Laurencia* (Ceramiales, Rhodophyta) para el archipiélago cubano. *Serie Oceanológica* 1: 104-107.
- BERNATOWICZ A. J. 1952. — Seasonal aspects of the Bermuda algal flora. *Papers of the Michigan Academy of Science, Arts & Letters* 36: 3-8.
- BØRGESEN F. 1915. — The marine algae of the Danish West Indies. Part 3. Rhodophyceae. *Dansk Botanisk Arkiv* 3: 1-80.
- BRUMMITT R. K. & POWELL C. E. 1992. — *Authors of Plant Names*. Royal Botanic Gardens, Kew, 732 p.
- CASSANO V., DÍAZ-LARREA J., SENTIES A., OLIVEIRA M. C., GIL RODRÍGUEZ M. C. & FUJII M. T. 2009. — Evidence for the conspecificity of *Palisada papillosa* with *P. perforata* (Ceramiales, Rhodophyta) from the western and eastern Atlantic Ocean on the basis of morphological and molecular analyses. *Phycologia* 48: 86-100. <https://doi.org/10.2216/0031-8884-48.2.86>
- CASSANO V., METTI Y., MILLAR A. J. K., GIL-RODRÍGUEZ M. C., SENTIES A., DÍAZ-LARREA J., OLIVEIRA M. C. & FUJII M. T. 2012a. — Redefining the taxonomic status of *Laurencia dendroidea* (Ceramiales, Rhodophyta) from Brazil and the Canary Islands. *European Journal of Phycology* 47: 67-81. <https://doi.org/10.1080/09670262.2011.647334>
- CASSANO V., OLIVEIRA M. C., GIL-RODRÍGUEZ M. C., SENTIES A., DÍAZ-LARREA J. & FUJII M. T. 2012b. — Molecular support for the establishment of the new genus *Laurenciella* within the *Laurencia* complex (Ceramiales, Rhodophyta). *Botanica Marina* 55: 349-357.
- CASSANO V., SANTOS G. N., PESTANA E. M. S., NUNES J. M. C., OLIVEIRA M. C. & FUJII M. T. 2019. — *Laurencia longiramea* sp. nov. for Brazil and an emendation of the generic delineation of *Corynecladia* (Ceramiales, Rhodophyta). *Phycologia* 58: 115-127. <https://doi.org/10.1080/00318884.2018.1523519>
- COLLADO-VIDES L., CASSANO V., DÍAZ-LARREA J., DURAN A., DA-SILVA-MEDEIROS A., SENTIES A & FUJII M. T. 2014. — Spread of the introduced species *Laurencia caduciramulosa* (Rhodomelaceae, Rhodophyta) to the northwest Atlantic: a morphological and molecular analysis. *Phytotaxa* 183 (2): 93-107.
- COLLADO-VIDES L., DURAN A., ARMENIS E., CASSANO V., BURKEPILLE D., SHANTZ A. A., PALMA L., DÍAZ-LARREA J., SENTIES A. & FUJII M. T. 2017. — Seasonal recruitment and survival strategies of *Palisada cervicornis* comb. nov. (Ceramiales, Rhodophyta) in coral reefs. *Journal of Phycology* 53: 1087-1096. <https://doi.org/10.1111/jpy.12567>
- COLLADO-VIDES L., CASSANO V., SANTOS G. N., SENTIES A. & FUJII M. T. 2018. — Molecular and morphological characterization of *Laurencia intricata* and *Laurenciella mayaimii* sp. nov. (Ceramiales, Rhodophyta) in South Florida, United States. *Phycologia* 57: 287-297. <https://doi.org/10.2216/17-80.1>
- COLLINS F. S. & HERVEY A. B. 1917. — The algae of Bermuda. *Proceedings of the American Academy of Arts & Sciences* 53: 1-195.
- COLLINS F. S., HOLDEN I. & SETCHELL W. A. 1912. — *Phycotheca Boreali-Americana (Exsiccata), Algae of North America*. Fascicle XXXVIII. Algae of Bermuda. Nos. 1851-1900. Malden, Massachusetts.
- COLLINS F. S., HOLDEN I. & SETCHELL W. A. 1913. — *Phycotheca Boreali-Americana (Exsiccata), Algae of North America*. Fascicle XXXIX. Algae of Bermuda. Nos. 1901-1950. Malden, Massachusetts.
- COLLINS F. S., HOLDEN I. & SETCHELL W. A. 1916. — *Phycotheca Boreali-Americana (Exsiccata), Algae of North America*. Fascicle XLII. Algae of Bermuda. Nos. 2051-2100. Malden, Massachusetts.
- COLLINS F. S., HOLDEN I. & SETCHELL W. A. 1917. — *Phycotheca*

- Boreali-Americana (Exsiccata), Algae of North America*. Fascicle XLIV. Algae of Bermuda. Nos. 2151-2200. Malden, Massachusetts.
- CORDEIRO-MARINO M. 1978. — Rodofíceas bentônicas marinhas do Estado de Santa Catarina. *Rickia* 7: 1-243.
- CRIBB A. B. 1958. — Records of marine algae from south-eastern Queensland. III. *Laurencia* Lamx. *University of Queensland Papers, Department of Botany* 3: 159-191.
- DARRIBA D., TABOADA G. L., DOALLO R. & POSADA D. 2012. — jModelTest 2: more models, new heuristics and parallel computing. *Nature Methods* 9: 772.
- DAWES C. J. & MATHIESON A. C. 2008. — *The Seaweeds of Florida*. University Press of Florida, Gainesville, Florida, 591 p.
- DÍAZ-LARREA J., SENTÍES A., FUJII M. T., PEDROCHE F. F. & OLIVEIRA M. C. 2007. — Molecular evidence for *Chondrophycus poiteaui* var. *gemmiferus* comb. et stat. nov. (Ceramiales, Rhodophyta) from the Mexican Caribbean: implications for the taxonomy of the *Laurencia* complex. *Botanica Marina* 50: 250-256. <https://doi.org/10.1515/BOT.2007.026>
- DICKIE G. 1874. — I. On the marine algae of St. Thomas and the Bermudas, and on *Halophila baillonis*, Asch., in HOOKER J. D., Contributions to the botany of the expedition of H.M.S. 'Challenger'. *Journal of the Linnean Society, Botany* 14: 311-317. <https://doi.org/10.1111/j.1095-8339.1874.tb00315.x>
- FIGUEIREDO M. A. O., BARRETO M. B. B. & REIS R. P. 2004. — Caracterização das macroalgas nas comunidades marinhas da área de Proteção Ambiental de Cairuçu, Parati, RJ - subsídios para futuros monitoramentos. *Revista Brasileira de Botânica* 27: 11-17.
- FREDERICK J. J. 1963. — *The Marine Algae of the Bermuda Platform*. Ph.D. dissertation, University of Michigan, Ann Arbor, 89 p.
- FUJII M. T., CASSANO V., STEIN E. M. & CARVALHO L. C. 2011. — Overview of the taxonomy and of the major secondary metabolites and their biological activities related to human health of the *Laurencia* complex (Ceramiales, Rhodophyta) from Brazil. *Revista Brasileira de Farmacognosia* 21: 268-282. <https://doi.org/10.1590/S0102-695X2011005000064>
- FUJII M. T., GUIMARÃES S. M. P. B., GURGEL C. & FREDERICQ S. 2006. — Characterization and phylogenetic affinities of the red alga *Chondrophycus flagelliferus* (Rhodomelaceae, Ceramiales) from Brazil on the basis of morphological and molecular evidence. *Phycologia* 45: 432-441. <https://doi.org/10.2216/04-33.1>
- FUJII M. T. & SENTÍES A. 2005. — Taxonomia do complexo *Laurencia* (Rhodomelaceae, Rhodophyta) do Brasil, com ênfase nas espécies dos estados de São Paulo e do Espírito Santo. *Monografias Ficológicas* 2: 69-112.
- GARBARY D. J. & HARPER J. T. 1998. — A phylogenetic analysis of the *Laurencia* complex (Rhodomelaceae) of the red algae. *Cryptogamie, Algologie* 19: 185-200.
- GIL-RODRÍGUEZ M. C., SENTÍES A., DÍAZ-LARREA J., CASSANO V. & FUJII M. T. 2009. — *Laurencia marilzae* sp. nov. (Ceramiales, Rhodophyta) from the Canary Islands, Spain, based on morphological and molecular evidence. *Journal of Phycology* 45: 264-271. <https://doi.org/10.1111/j.1529-8817.2008.00624.x>
- GIL-RODRÍGUEZ M. C., CASSANO V., AYLAGAS E., SENTÍES A., DÍAZ-LARREA J., OLIVEIRA M. C. & FUJII M. T. 2010. — *Palisada flagellifera* (Ceramiales, Rhodophyta) from the Canary Islands, Spain: a new record for the eastern Atlantic Ocean based on morphological and molecular evidence. *Botanica Marina* 53: 31-40. <https://doi.org/10.1515/BOT.2010.010>
- GUIRY M. D. & GUIRY G. M. 2020. — AlgaeBase, world-wide electronic publication, National University of Ireland, Galway. <http://www.algaebase.org>, accessed on 24 July 2020.
- HARVEY W. H. 1853. — Nereis boreali-americana. Part II. — Rhodospereae. *Smithsonian Contributions to Knowledge* 5 (5): 1-258, pls. XIII-XXXVI.
- HEMSLEY W. B. 1884. — Algae, i, ii, in, *Report of the Botany of the Bermudas and Various Other Islands of the Atlantic and Southern Oceans Report of the Scientific Research of the Exploring Voyage of H.M.S. "Challenger," 1873-1876*. *Botany* 1 (2): 1-135.
- HOWE M. A. 1918. — Algae. in Britton N. L. (ed.), *Flora of Bermuda*. Charles Scribner's Sons, New York, 585 p.
- KEMP A. F. 1857. — Notes on the Bermudas and their natural history, with special reference to their marine algae. *Canadian Naturalist and Geologist* 2: 145-156.
- KÜTZING F. T. 1865. — *Tabulae phycologicae*. Vol. 15. Gedruckt auf Kosten des Verfassers (in commission bei W. Köhne), Nordhausen, Germany, 36 p.
- LAMOUREUX J. V. F. 1813. — Essai sur les genres de la famille des thalassiphytes non articulées. *Annales du Muséum d'histoire naturelle, Paris* 20: 131-132.
- LE GALL L. & SAUNDERS G. W. 2010. — DNA barcoding is a powerful tool to uncover algal diversity: a case study of the Phylloporaceae (Gigartinales, Rhodophyta) in the Canadian flora. *Journal of Phycology* 46: 374-389. <https://doi.org/10.1111/j.1529-8817.2010.00807.x>
- LITTLER D. S. & LITTLER M. M. 2000. — *Caribbean Reef Plants. An Identification Guide to the Reef Plants of the Caribbean, Bahamas, Florida and Gulf of Mexico*. Offshore Graphics, Washington, 542 p.
- MACHÍN-SÁNCHEZ M., CASSANO V., DÍAZ-LARREA J., SENTÍES A., FUJII M. T. & GIL-RODRÍGUEZ M. C. 2012. — Morphological and molecular evidence demonstrates the amphi-Atlantic distribution of *Laurencia catarinensis* (Ceramiales, Rhodophyta). *Botanica Marina* 55: 241-252. <https://doi.org/10.1515/bot-2011-0049>
- MACHÍN-SÁNCHEZ M., GIL-RODRÍGUEZ M. & HAROUN R. 2018. — Phylogeography of the red alga *Laurencia* complex in the Macaronesia region and nearby coastal areas: recent advances and future perspectives. *Diversity* 10: 1-21. <https://doi.org/10.3390/d10010010>
- MARTIN-LESCANNE J., ROUSSEAU F., DE REVIERS B., PAYRI C., COULOUX A., CRUAUD C., & LE GALL L. 2010. — Phylogenetic analyses of the *Laurencia* complex (Rhodomelaceae, Ceramiales) support recognition of five genera: *Chondrophycus*, *Laurencia*, *Osmundea*, *Palisada* and *Yuzurua* stat. nov. *European Journal of Phycology* 45: 51-61. <https://doi.org/10.1080/09670260903314292>
- MASUDA M., KAWAGUCHI S., TAKAHASHI Y., MATSUI Y. & SUZUKI M. 1997. — A taxonomic study of the genus *Laurencia* (Ceramiales, Rhodophyta) from Vietnam. I. *Laurencia caduciramulosa* Masuda & Kawaguchi, sp. nov. *Cryptogamie, Algologie* 18: 1-10.
- MATEO-CID E. L., MENDOZA-GONZALEZ A. C., SENTÍES A., DÍAZ-LARREA J. & CALDERÓN J. A. A. 2014. — *Laurencia laurahuertana* sp. nov. (Rhodomelaceae, Rhodophyta): An epiphytic species from the Mexican Caribbean. *Phycological Research* 62: 94-101. <https://doi.org/10.1111/pre.12043>
- MCIVOR L., MAGGS C. A., GUIRY M. D. & HOMMERSAND M. H. 2002. — Phylogenetic analysis of the geographically disjunct genus *Osmundea* Stackhouse (Rhodomelaceae, Rhodophyta). *Constancea* 83:9.
- METTI Y., MILLAR A. J. K. & STEINBERG P. 2015. — A new molecular phylogeny of the *Laurencia* complex (Rhodophyta, Rhodomelaceae) and a review of key morphological characters results in a new genus: *Coronaphycus*, and a description of *C. novus*. *Journal of Phycology* 51: 929-942. <https://doi.org/10.1111/jpy.12333>
- MONTAGNE C. 1842. — Botanique. Plantes cellulaires, in SAGRA R. de la (ed.), *Histoire physique, politique et naturelles de l'île de Cuba*. Vol. 11: 549 p.
- MURRAY G. 1888. — Catalogue of the marine algae of the West Indian region. I.-Florideae, II.-Phaeophyceae. *Journal of Botany, British and Foreign* 26: 193-196; 237-243, 303-307; 331-338; 358-363.
- NAM K. W. 1999. — Morphology of *Chondrophycus undulata* and *C. parvipapillata* and its implications form the taxonomy of the *Laurencia* (Ceramiales, Rhodophyta) complex. *European Journal of Phycology* 34: 455-468. <https://doi.org/10.1080/09541449910001718811>
- NAM K. W. 2006. — Phylogenetic re-evaluation of the *Laurencia* complex (Rhodophyta) with a description of *L. succulenta* sp. nov. from Korea. *Journal of Applied Phycology* 18: 679-607. <https://doi.org/10.1007/s10801-006-9070-7>

- doi.org/10.1007/s10811-006-9073-3
- NAM K. W. 2007. — Validation of the generic name *Palisada* (Rhodomelaceae, Rhodophyta). *Algae* 22: 53-55. <https://doi.org/10.4490/ALGAE.2007.22.2.053>
- NAM K. W., CHOI H. G., LEE S., PARK E. J., KANG K. H. & KIM Y. S. 2000. — Vegetative and reproductive development of *Laurencia venusta* (Ceramiales, Rhodophyta). *Cryptogamie, Algologie* 21: 97-110. [https://doi.org/10.1016/S0181-1568\(00\)00109-4](https://doi.org/10.1016/S0181-1568(00)00109-4)
- NAM K. W., MAGGS C. A. & GARBARY D. J. 1994. — Resurrection of the genus *Osmundea* with an emendation of the generic delineation of *Laurencia* (Ceramiales, Rhodophyta). *Phycologia* 33: 384-395. <https://doi.org/10.2216/i0031-8884-33-5-384.1>
- NAM K. W. & SOHN C. H. 1994. — *Laurencia kangjaewonii* sp. nov. (Ceramiales, Rhodophyta) from Korea. *Phycologia* 33: 397-403. <https://doi.org/10.2216/i0031-8884-33-6-397.1>
- OLIVEIRA FILHO E. C. 1977. — *Algas Marinhas Bentônicas do Brasil*. Tese de Livre Docência, Universidade de São Paulo, São Paulo, 407 p.
- PINHEIRO-JOVENTINO F., DANTAS N. P. & MARASCHIN C. D. H. 1998. — Distribuição de algas marinhas no litoral de Fortaleza, Ceará, Brasil. *Arquivos de Ciências do Mar* 31: 29-40.
- POPOLIZIO T. R., SCHNEIDER C. W., CHENG SUPANIMIT T., SAUNDERS G. W. & LANE C. E. 2013. — Notes on the marine algae of the Bermudas. 13. *Helminthocladia kempii* sp. nov. (Nemaliales, Liagoraceae) based upon *H. calvadosii sensu auct.* from the western Atlantic. *Cryptogamie, Algologie* 34: 229-44. <https://doi.org/10.7872/crya.v34.iss3.2013.229>
- REIN J. J. 1873. — Über die Vegetations-Verhältnisse der Bermudas-Inseln. *Bericht über die Senckenbergische Naturforschende Gesellschaft in Frankfurt am Main, 1872-1873*: 131-153.
- ROCHA-JORGE R., CASSANO V., OLIVEIRA M. C. & FUJII M. T. 2010. — The occurrence of *Laurencia marilzae* (Ceramiales, Rhodophyta) in Brazil based on morphological and molecular data. *Botanica Marina* 53: 143-162. <https://doi.org/10.1515/BOT.2010.018>
- RONQUIST F. & HUELSENBECK J. P. 2003. — MrBayes 3: Bayesian phylogenetic inference under mixed models. *Bioinformatics* 19: 1572-1574.
- ROUSSEAU F., GEY D., KURIHARA A., MAGGS C. A., MARTIN-LESCANNE J., PAYRI C., DE REVIERS B., SHERWOOD A. R. & LE GALL L. 2017. — Molecular phylogenies support taxonomic revision of three species of *Laurencia* (Rhodomelaceae, Rhodophyta), with the description of a new genus. *European Journal of Taxonomy* 269: 1-19.
- SAITO Y. 1964. — Contributions to the morphology of the genus *Laurencia* of Japan. I. *Bulletin of the Faculty of Fisheries, Hokkaido University* 15: 69-74.
- SAITO Y. 1967. — Studies on Japanese species of *Laurencia*, with special reference to their comparative morphology. *Memoirs of the Faculty of Fisheries, Hokkaido University* 15: 1-81.
- SAITO Y. 1969. — The algal genus *Laurencia* from the Hawaiian Islands, the Philippine Islands and adjacent areas. *Pacific Science* 23: 148-160.
- SAITO Y. 1982. — Morphology and infrageneric position of three British species of *Laurencia* (Ceramiales, Rhodophyta). *Phycologia* 21: 299-306. <https://doi.org/10.2216/i0031-8884-21-3-299.1>
- SAUNDERS G. W. & McDEVIT D. C. 2012. — Methods for DNA barcoding photosynthetic protists emphasizing the macroalgae and diatoms. *Methods in Molecular Biology* 858: 207-222.
- SAUNDERS G. W. & DRUEHL L. 1993. — Revision of the kelp family Alariaceae and the taxonomic affinities of *Lessoniopsis* Reinke. *Hydrobiologia* 260/261: 689-697.
- SAUNDERS G. W. & MOORE T. E. 2013. — Refinements for the amplification and sequencing of red algal DNA barcode and RedToL phylogenetic markers: a summary of current primers, profiles and strategies. *Algae* 28: 31-43. <https://doi.org/10.4490/algae.2013.28.1.031>
- SCHMITZ F. 1889. — Systematische Übersicht der bisher bekannten Gattungen der Florideen. *Flora oder Allgemeine botanische Zeitung* 72: 435-456.
- SCHNEIDER C. W. 2003. — An annotated checklist and bibliography of the marine macroalgae of the Bermuda islands. *Nova Hedwigia* 76: 275-361. <https://doi.org/10.1127/0029-5035/2003/0076-0275>
- SCHNEIDER C. W. & LANE C. E. 2005. — Notes on the marine algae of the Bermudas. 7. Additions to the flora including *Chondracanthus saundersii* sp. nov. (Rhodophyta, Gigartinaceae) based upon *rbcl* sequence analysis. *Phycologia* 44: 72-83. [https://doi.org/10.2216/0031-8884\(2005\)44\[72:NOTMAO\]2.0.CO;2](https://doi.org/10.2216/0031-8884(2005)44[72:NOTMAO]2.0.CO;2)
- SCHNEIDER C. W. & LANE C. E. 2007. — Notes on the marine algae of the Bermudas. 8. Further additions to the flora, including *Griffithsia aestivana* sp. nov. (Ceramiaceae, Rhodophyta) and an update on the alien *Cystoseira compressa* (Sargassaceae, Heterokontophyta). *Botanica Marina* 50: 128-140.
- SCHNEIDER C. W., LANE C. E. & SAUNDERS G. W. 2010. — Notes on the marine algae of the Bermudas. 11. More additions to the benthic flora and a phylogenetic assessment of *Halymenia pseudofloresii* Collins & M. Howe (Halymeniales, Rhodophyta) from its type locality. *Phycologia* 46: 154-168. <https://doi.org/10.2216/PH09-46.1>
- SENTÍAS A., CASSANO V., DRECKMANN K. M., GIL-RODRÍGUEZ, M. C. & STEIN E. M. & FUJII M. T. 2016. — *Chondrophycus anabeliae* (Rhodomelaceae, Ceramiales), a new species in the *Laurencia* complex from the Mexican Caribbean. *Phytotaxa* 283 (3): 259-270. <https://doi.org/10.11646/phytotaxa.283.3.2>
- SENTÍAS A. & DÍAZ-LARREA J. 2008. — Proposals for *Palisada poiteaui* var. *gemmifera* comb. nov. and *Palisada corallopsis* comb. nov. (Rhodomelaceae, Rhodophyta). *Botanica Marina* 51: 69-70. <https://doi.org/10.1515/BOT.2008.004>
- SENTÍAS A., DÍAZ-LARREA J., CASSANO V., GIL-RODRÍGUEZ M. C. & FUJII M. T. 2011. — *Laurencia marilzae* (Ceramiaceae, Rhodophyta) from the Mexican Caribbean: a new record for the tropical western Atlantic. *Bulletin of Marine Science* 87: 681-686. <https://doi.org/10.5343/bms.2010.1094>
- SENTÍAS A., DRECKMANN K. M., HERNÁNDEZ O. E., NÚÑEZ RESENDIZ M. L., LE GALL L. & CASSANO V. 2019. — Diversity and distribution of *Laurencia sensu stricto* (Rhodomelaceae, Rhodophyta) from the Mexican Pacific, including *L. mutuae* sp. nov. *Phycological Research* 67: 267-278. <https://doi.org/10.1111/pre.12382>
- SENTÍAS A., FUJII M. T. & RODRÍGUEZ D. 2001. — *Laurencia venusta* (Ceramiaceae, Rhodophyta): a new record from the Atlantic Ocean. *Botanica Marina* 44: 95-99. <https://doi.org/10.1515/BOT.2001.013>
- SENTÍAS A., WYNNE M. J., CASSANO V., GIL-RODRÍGUEZ M. C. & FUJII M. T. 2015. — *Yuzurua iridescens* (M.J. Wynne & D.L. Ballantine) comb. nov. (Ceramiaceae, Rhodophyta) from the Caribbean Sea: morphological and molecular evidence. *Brazilian Journal of Botany* 38: 605-613. <https://doi.org/10.1007/s40415-015-0154-x>
- SILVESTRO D. & MICHALAK I. 2011 [2012]. — raxmlGUI: a graphical front-end for RAXML. *Organisms Diversity & Evolution* 12: 335-337.
- STACKHOUSE J. 1809. — Tentamen marino-cryptogamicum, ordinem novum, in genera et species distributum, in Classe XXIVta Linnaei sistens. *Mémoires de la Société Impériale des Naturalistes de Moscou* 2: 50-97.
- TANDY G. 1936. — Marine algae. In: Rendle A.B.: Notes on the flora of the Bermudas. *Journal of Botany, British and Foreign* 74: 42-50, 65-71, 101-112.
- TAYLOR W. R. 1960. — *Marine Algae of the Eastern Tropical and Subtropical Coasts of the Americas*. Univ. Michigan Press, Ann Arbor, 870 p.
- TSENG C. K. 1943. — Marine algae of Hong Kong. IV The genus *Laurencia*. *Papers of the Michigan Academy of Science, Arts & Letters* 28: 185-208.
- WOMERSLEY H. B. S. 2003. — *The Marine Benthic Flora of Southern*

Australia - Part IIID Ceramiales - Delesseriaceae, Sarcomeniaceae, Rhodomelaceae., Australian Biological Resources Study & State Herbarium of South Australia, Canberra & Adelaide, 533 p.

YAMADA Y. 1931. — Notes on *Laurencia*, with special reference to the Japanese species. *University of California Publications in Botany* 16: 185-311.

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APPENDICES

APPENDIX 1. — Collection details and GenBank accession numbers for isolates included in the molecular analyses of this study. Newly generated GenBank numbers in **bold** type. For both COI-5P and *rbcL* genes, we selected one specimen of each newly sequenced species and geographic location for deposit in GenBank. The complete datasets for each gene can be shared upon request. At present, sequence data provided to us from the following are not publicly available: **M. Fujii, **** V. Cassano.

| Taxa | Voucher/ Collection data | COI-5P Accession numbers | <i>rbcL</i> Accession numbers |
|---|--|--------------------------------|-------------------------------------|
| <i>Acanthophora spicifera</i> (Vahl) Børgesen | India, Tamil Nadu coast | – | MT478065 |
| <i>Acanthophora</i> sp. | Australia, Western Australia, Rottnest Island, 15.III.2015 | – | MF094033 |
| <i>Alsidium corallinum</i> C.Agardh | Spain, Canary Islands, Lanzarote, 13.VI.2018, P. Diaz-Tapia | – | MN165090 |
| <i>Alsidium oliveiranum</i> S.M.Guim. & M.T.Fujii | Brazil, Espirito Santo, Anchieta, Parati Beach, 4.X.2006, M. Fujii | – | MN165086 |
| <i>Alsidium seaforthii</i> (Turner) J.Agardh | United States, Florida, Fort Pierce, 10.VIII.2013, G. Garcia-Soto | – | MH204657 |
| <i>Alsidium triquetrum</i> (S.G.Gmel.) Trevis. | Venezuela, Falcon, Playa Buchuacos, 10.VI.2012, G. Garcia-Soto | – | MH204654 |
| <i>Bortrychia calliptera</i> (Mont.) Mont. | Mexico, Sontecomapan, Vera Cruz, 10.II.1994, J. West & G. Zuccarello | – | AY920806 |
| <i>Bostrychia mixta</i> J.D.Hook. & Harv. | Saint Helena, Nightingale, Seal Pool and naer shore, 21.III.2010, S. Scott | – | MK185794 |
| <i>Bostrychia mortiziana</i> (Kütz.) J.Agardh | Indonesia, West Sawang, Sulawesi, 16.XI.1994, J. West & G. Zuccarello | – | AY920813 |
| <i>Bostrychia radicans</i> (Mont.) Mont. | United States, Mississippi, St. Louis Bay, 11.II.1998, F. Gurgel | – | AF259497 |
| <i>Bostrychia tenella</i> (J.V.Lamour.) J.Agardh | American Samoa, Tutuila, 26.VII.1991, B. Rainey | – | AY920836 |
| <i>Coeloclonium umbellatum</i> (Harv.) J.Agardh | Australia, Western Australia, Rottnest Island, 15.III.2015 | – | MF094052 |
| <i>Coeloclonium</i> sp. | Australia, South Australia, Port MacDonnell, 28.VIII.1995, M. Hommersand | – | MH388575 |
| <i>Chondria baileyana</i> (Mont.) Harv. | Canada, Prince Edward I., Pownal, 29.VII.2008, G. Saunders | – | KU564500 |
| <i>Chondria californica</i> (Collins) Kylin | United States, California, San Diego Co., Beach Club Reef, La Jolla Shores, 1.VII.1996, M. Volovsek | – | AY172578 |
| <i>Chondria collinsiana</i> M.Howe | Brazil, Rio de Janeiro, Armacao dos Buzios, Praia Rasa, 13.I.2005, V. Cassano & J. De-Paula | – | AF259497 |
| <i>Chondria dasyphylla</i> (Woodw.) C.Agardh | United States, North Carolina, Carteret Co., Bogue Sound, W. Freshwater | – | U04021 |
| <i>Chondria succulenta</i> (J.Agardh) Falkenb. | Australia, New South Wales, Batehaven, 30.V.2005, Y. Metti | – | KY120336 |
| <i>Chondrophycus anabeliae</i> Senties, M.T.Fujii, Cassano & Dreckmann | Mexico, Quintana Roo, Isla Mujeres, 12.II.2007, A. Senties & M. Gil- Rodriguez | – | KX815262 |
| <i>Chondrophycus dotyi</i> (Y.Saito) K.W.Nam | United States, Hawaii, A. Sherwood (ARS01606) | HQ422621 | – |
| <i>Chondrophycus dotyi</i> | United States, Hawaii, Oahu, Sandy Beach, 31.V.2015, E. Stein | – | KX815263 |
| <i>Chondrophycus planiparvus</i> Popolizio, C.W.Schneid. & C.E.Lane sp. nov. | Bermuda, Gurnet Rock, mouth of Castle Harbour, 13.III.2012, T. Popolizio; Holotype: BDA 0934 [TRP 12-40-13] | OK209884 | OK209859 |
| <i>Chondrophycus tronoi</i> (Ganzon- Fortes) K.W.Nam | Philippines, A. Lluisma | – | AF489864 |
| <i>Chondrophycus undulatus</i> (Yamada) Garbary & J.T.Harper | United States, Hawaii, A. Sherwood (ARS02922) | HQ422996 | – |
| <i>Chondrophycus undulatus</i> | United States, Hawaii, A. Sherwood (ARS02493) | HQ422752 | – |
| <i>Chondrophycus undulatus</i> | United States, Hawaii, A. Sherwood (ARS00733) | HQ423055 | – |
| <i>Chondrophycus cf. undulatus</i> | New Caledonia, Loyalty Island, Mare, 22.III.2005, C. Payri | – | FJ785307 |
| <i>Chondrophycus</i> sp. | Australia, Norfolk Island, Collins Head, 21.III.2005, Y. Metti & A. Millar | – | KY120338 |
| <i>Chondrophycus</i> sp. | South Africa, KwaZulu-Natal, Sodwana Bay, Jesser Point, 9.VI.2010, R. Anderson & J. Bolton | – | KY927795 |
| <i>Chondrophycus</i> sp. | United States, Texas, Flower Garden Banks Sanctuary, II.2000, S. Fredericq | – | AF465817 |
| <i>Chondrophycus</i> sp. 1 | New Caledonia, Loyalty Island, Lifou, 26.III.2005, C. Payri | – | FJ785309 |
| <i>Chondrophycus</i> sp. 2 | New Caledonia, Loyalty Island, Mare, 21.III.2005, C. Payri | – | FJ785310 |
| <i>Chondrophycus</i> sp. 3 | New Caledonia, Loyalty Island, Beautemps/Beaupre, 6.IV.2005, C. Payri | – | FJ785311 |
| <i>Corynecladia clavata</i> (Sond.) C.Agardh | Australia, Victoria, Walkerville, 20.I.2015, P. Diaz-Tapia & M. Brookes | – | MF094079 |
| <i>Corynecladia clavata</i> | Australia: Victoria, The Caves, 21.I.2015, P. Diaz-Tapia & M. Brookes | MH704456 | – |
| <i>Corynecladia elatus</i> (C.Agardh) Cassano, M.C.Oliveira & M.T.Fujii | Australia, Western Australia, Rottnest Island, 15.XI.2008, J. Eu | – | KY120339 |
| <i>Corynecladia nova</i> (Metti) Cassano, M.C.Oliveira & M.T.Fujii | Australia, NSW, Jervis Bay, Plantation Pt, subtidal, 15.II.2005, Y. Metti & A. Millar | – | KY120340 |
| <i>Digenea mexicana</i> G.H.Boo & D.Robledo | Mexico, Playa Xcalococo, Quintana Roo, 19.IV.2018, D. Robledo | – | MH514862 |
| <i>Digenea rafaellii</i> G.H.Boo, G.Andrade- Sorcía & S.M.Boo | Mexico, Bahia de Kino, La Cruses, Sonora, 16.V.2010, S.M. Boo & R. Riosmena-Rodriguez | – | MH514867 |
| <i>Digenea simplex</i> (Wulfen) C.Agardh | Greece, Saronikos, Gourkolimano, 12.IV.2011, F. Kuepper | – | MH388507 |
| <i>Digenea</i> sp. | Japan, Sesoko Island, Okinawa, 30.VII.2009 | – | MH514872 |

APPENDIX 1. — Continuation.

| Taxa | Voucher/ Collection data | COI-5P Accession numbers | rbcl Accession numbers |
|--|---|--------------------------------|------------------------------|
| <i>Laurencia alfredensis</i> C.Francis, J.J.Bolton, Mattio & R.J.Anderson | South Africa, Western Cape, Grootbank, 4.VII.2008, R. Anderson & J. Bolton | – | KY927749 |
| <i>Laurencia</i> cf. <i>brongiartii</i> J.Agardh | Australia, Western Australia, Tarcoola Beach, 1993, S. Fredericq | – | EF061654 |
| <i>Laurencia</i> cf. <i>brongiartii</i> | Taiwan, Makang Harbour, 11.VII.1993, S. Fredericq | – | AF465814 |
| <i>Laurencia caduciramulosa</i> Masuda & S.Kawaguchi | Spain, Canary Islands, Tenerife, Punta del Hidalgo, 6.V.2008, M. Gil-Rodríguez, M. Fujii, V. Cassano & J. Díaz-Larrea | – | JF781525 |
| <i>Laurencia caduciramulosa</i> | United States, Florida, Key Biscayne, Crandon Park, 13.VIII.2013, L. Collado-Vides, A. Duran, M. Fujii, V. Cassano & J. Díaz-Larrea | – | KJ700867 |
| <i>Laurencia caduciramulosa</i> | Cuba, Havana, Rincon de Guanabo, 2002, A. Areces | – | FJ904933 |
| <i>Laurencia caduciramulosa</i> | Brazil, Rio de Janeiro, Angra dos Reis, Praia do Velho, 19.IV.2006, V. Cassano & J.C. De-Paula | – | KJ700865 |
| <i>Laurencia</i> cf. <i>calliptera</i> Kütz. | New Caledonia, Ile des Pins, 2.XII.2005, C. Payri | KX258825 | – |
| <i>Laurencia caraibica</i> P.C.Silva | Mexico, Quintana Roo, Cancún, Isla Mujeres, 2006, A. Sentíes | – | EF658642 |
| <i>L. catarinensis</i> Cordeiro-Marino & M.T.Fujii | Brazil, Rio Grande do Norte, Maracajau, 24.VI.2006, M. Fujii & I. Silva | – | ** |
| <i>Laurencia catarinensis</i> | Bermuda, St. David's I., Fort Hill Bay, Cooper's Island, 27.V.2012, T. Popolizio; BDA 1130 [TRP 12-65-2] | OK209904 | OK209872 |
| <i>Laurencia catarinensis</i> | United States, Florida, Key West, East Dry Rocks Reef, 30.V.2013, C. Schneider, C. Lane & T. Popolizio; KW 208 [CWS/CEL/TRP 13-13-16] | OK209903 | OK209873 |
| <i>Laurencia catarinensis</i> | US Virgin Islands, St. Croix, Fredericksted Pier, 24.XI.2013, T. Popolizio & E. Salomaki; STX 222 [TRP 13-40-5] | OK209898 | OK209874 |
| <i>Laurencia catarinensis</i> | Spain, Canary Islands, Lanzarote, Pechiguerras, 15.I.2013, M. Gil-Rodríguez & M. Machin-Sanchez | KF492718 | – |
| <i>Laurencia catarinensis</i> | Spain, Canary Islands, Tenerife, El Pris, 3.II.2011, M. Machin-Sanchez | – | KF492776 |
| <i>Laurencia catarinensis</i> | Spain, Canary Islands, Lanzarote, Arrecife, 18.X.2012, J. Martin, M. Carrillo Perez | – | KF492780 |
| <i>Laurencia complanata</i> (Suhr) Kütz. | South Africa, KwaZulu-Natal, Salt Rock, 9.XII.2010, R. Anderson & J. Bolton | – | KY927738 |
| <i>Laurencia corymbosa</i> J.Agardh | South Africa, Eastern Cape, Double Mouth, 14.VII.2010, R. Anderson & J. Bolton | – | KY927728 |
| <i>Laurencia dendroidea</i> J.Agardh | Brazil, Sao Paulo, Ubatuba, Praia do Felix, 31.VIII.2000, M. Fujii | – | AF465810 |
| <i>Laurencia dendroidea</i> | Brazil, Rio de Janeiro, Ponta do Caioba, Angra dos Reis, 2004, V. Cassano | – | GU330223 |
| <i>Laurencia dendroidea</i> | Bermuda, Middle buoy, Eastern Blue Cut channel, north of Daniel's Head, Somerset Is., 20.VIII.2010, C. Schneider, C. Lane & T. Popolizio; BDA 0137 [CWS/CEL 10-12-38] | OK209900 | OK209876 |
| <i>Laurencia dendroidea</i> | United States, Florida, Key West, Fort Zachary Taylor, 28.V.2013, C. Schneider, C. Lane, D. McDevit & T. Popolizio; KW 064 [CWS/CEL/ TRP 13-7-2] | OK209901 | OK209875 |
| <i>Laurencia dendroidea</i> | US Virgin Islands, St. Croix, Salt River Bay, 21.XI.2013, C. Lane, T. Popolizio & E. Salomaki; STX 111 [CEL/TRP 13-30-2] | OK209899 | OK209877 |
| <i>Laurencia dendroidea</i> | United States, Hawaii, Molokai, 10.II.2007, A. Sherwood (ARS02692) | GU223887 | – |
| <i>Laurencia dendroidea</i> | Australia, Western Australia, Little Turtle, 15.V.2008, J. Huisman | MT822859 | – |
| <i>Laurencia dendroidea</i> | Australia, New South Wales, Batehaven, Batemans Bay, Observation Point, 30.V.2005, Y. Metti | MT822855 | – |
| <i>Laurencia dendroidea</i> | Australia, New South Wales, Arrawara Headland, 28.VII.2004, Y. Metti | MT822858 | – |
| <i>Laurencia dendroidea</i> | Australia, Norfolk Island, Little Organ off Captain Cook Memorial, 18.III.2005, Y. Metti | MT822857 | – |
| <i>Laurencia dendroidea</i> | Australia, New South Wales, Batehaven, Batemans Bay, Observation Point, 25.X.2005, Y. Metti & A. Millar | MT822856 | – |
| <i>Laurencia dendroidea</i> | Spain, Canary Islands, Lanzarote, Pechiguerras, 15.I.2013, M. Gil-Rodríguez & M. Manchin-Sanchez | KF492728 | – |
| <i>Laurencia dendroidea</i> | Spain, Canary Islands, La Gomera, Punta de La Dama, 21.IX.2009, E. Aylagas & M. Manchin-Sanchez | KF492725 | – |
| <i>Laurencia dendroidea</i> | Spain, Canary Islands, Tenerife, Puerto Cruz, 13.VII.2006, M. Gil- Rodríguez, M. Fujii & M. Manchin-Sanchez | – | EF686000 |
| <i>Laurencia dendroidea</i> | Venezuela, Falcon, Playa Buchuacos, 6.X.2012, G. Garcia-Soto | MH388711 | – |
| <i>Laurencia dichotoma</i> C.Francis, J.J.Bolton, Mattio & R.J.Anderson | South Africa, KwaZulu-Natal, Sodwana Bay, Jesser Point, 22.III.2011, J. Bolton, R. Anderson & C. Francis | – | KY927786 |
| <i>Laurencia digitata</i> C.Francis, J.J.Bolton, Mattio & R.J.Anderson | South Africa, Western Cape, De Hoop, East of Koppie Alleen, 18.II.2011, C. Francis, R. Anderson & J. Bolton | – | KY927779 |
| <i>Laurencia filiformis</i> (C.Agardh) Mont. | Australia, Western Australia, Tarcoola Beach, 21.IX.1995, M. Hommersand & F. Hommersand | – | MH704449 |
| <i>Laurencia flexuosa</i> Kütz. | South Africa, S. KwaZulu-Natal, Palm Beach, 7.II.2001, S. Fredericq | – | AF465815 |
| <i>Laurencia glomerata</i> Kütz. | South Africa, Western Cape, Mauritz Bay, 2.III.2011, M. Rothmann, C. Boothroyd & F. Kemp | – | KY927793 |
| <i>Laurencia intricata</i> J.V.Lamour. | Cuba, Ciego de Avila, Cayo Coco, 25.IX.2005, M. Fujii | – | GU330238 |

APPENDIX 1. — Continuation.

| Taxa | Voucher/ Collection data | COI-5P Accession numbers | rbcl Accession numbers |
|--|--|--------------------------------|------------------------------|
| <i>Laurencia intricata</i> | Bermuda, Bermuda I., Fairyland Creek, 25.VIII.2010, C. Schneider, C. Lane & T. Popolizio; BDA 0483 [CWS/CEL 10-32-5] | OK209897 | OK209879 |
| <i>Laurencia intricata</i> | United States, Florida, Key West, White Street Pier, 29.V.2013, C. Schneider, C. Lane, D. McDevit & T. Popolizio; KW 131 [CWS/CEL/TRP 13-9-23] | OK209906 | OK209878 |
| <i>Laurencia intricata</i> | United States, Florida, Key Biscayne, Crandon Park, 13.VIII.2013, L. Collado-Vides, V. Cassano & M. Fujii | – | MG004180 |
| <i>Laurencia intricata</i> | United States, Florida, Key Biscayne, Crandon Park, 13.VIII.2013, L. Collado-Vides, V. Cassano & M. Fujii | – | MG004181 |
| <i>Laurencia intricata</i> | US Virgin Islands, St. Croix, Deep Wrecks, 19.XI.2013, C. Lane, T. Popolizio & E. Salomaki; STX 010 [CEL/TRP 13-23-9] | – | OK209882 |
| <i>Laurencia intricata</i> | Mexico, Quintana Roo, Playa del Carmen, 2002, J. Díaz-Larrea & A. Senties | – | GQ149489 |
| <i>Laurencia intricata</i> | Mexico, Quintana Roo, Puerto Morelos, Ojo Agua, 2004, J. Díaz-Larrea & A. Senties | – | EF658644 |
| <i>Laurencia karachiana</i> Bibi, V.Cassano & Rasheed | Pakistan, Karachi, Buleji, 13.VIII.2018, R. Bibi | MK796229 | MK796228 |
| <i>Laurencia cf. kuetzingii</i> A.Millar | New Caledonia, Loyalty Is., Ouvea, 31.III.2005, C. Payri | – | FJ785322 |
| <i>Laurencia laurahuertana</i> Mateo-Cid, Mendoza-Gonzalez, Senties & Díaz-Larrea | Mexico, Quintana Roo, Punta Herrero, 2012, A. Mendoza-Gonzalez & L. Mateo-Cid | – | KF279401 |
| <i>Laurencia longiramea</i> Cassano, G.N.Santos, J.M.C.Nunes, M.C.Oliveira & M.T.Fujii | Brazil, Bahia, Marau, Barra Grande, Praia de Três Coqueiros, 28.IX.2015, G. Santos, E. Pestana & J. Nunes | – | MH704450 |
| <i>Laurencia longiramea</i> | Brazil, Espirito Santo, Anchieta, Ilhote de Ubu, 30.VI.2007, E. Stein | MH704454 | – |
| <i>Laurencia majuscula</i> (Harv.) A.H.S.Lucas | Oman, Dhofar, IX.2001, M. Wynne | KX258827 | – |
| <i>Laurencia cf. majuscula</i> | New Caledonia, Ile des Pins, 2.XII.2005, C. Payri | – | FJ785312 |
| <i>Laurencia cf. mariannensis</i> Yamada | New Caledonia, Lagon Sud-Ouest, Ilot Laregnere, 11.VII.2003, C. Payri | – | FJ785313 |
| <i>Laurencia mcdermidiae</i> I.A.Abbott | United States, Hawaii, Oahu, 8.IV.2007 | GU223878 | – |
| <i>Laurencia mcdermidiae</i> | United States, Hawaii, A. Sherwood (ARS03611) | HQ422883 | – |
| <i>Laurencia mcdermidiae</i> | United States, Hawaii, A. Sherwood (ARS00702) | HQ422627 | – |
| <i>Laurencia mcdermidiae</i> | United States, Hawaii, A. Sherwood (ARS02003) | HQ423053 | – |
| <i>Laurencia cf. mcdermidiae</i> | New Caledonia, Ile des Pins, 29.XI.2005, C. Payri | – | F7J85314 |
| <i>Laurencia microcladia</i> Kütz. | Bermuda, south shore Bermuda I., Capt. Williams' Bay, 15.I.2012, C. Schneider, C. Lane & T. Popolizio; BDA 0523 [CWS/CEL/TRP 12-2-2] | OK209905 | OK209880 |
| <i>Laurencia microcladia</i> | US Virgin Islands, St. Croix, Turtle Deli Beach, 20.XI.2013, C. Lane, T. Popolizio & E. Salomaki; STX 079 [CEL/TRP 13-26-2] | OK209896 | OK209881 |
| <i>Laurencia multiclavata</i> C.Francis, J.J.Bolton, Mattio & R.J.Anderson | South Africa, KwaZulu-Natal, Sodwana Bay, Jesser Point, 22.III.2011, J. Bolton, R. Anderson & C. Francis | – | KY927789 |
| <i>Laurencia mutuae</i> Senties, Cassano & Dreckmann | Mexico, Acapulco, Guerrero, Isla la Roqueta, 7.VI.2017, A. Senties & K. Dreckmann | MK182534 | MK159179 |
| <i>Laurencia natalensis</i> Kylin | South Africa, S. KwaZulu-Natal, Palm Beach, 7.II.2001, S. Fredericq | – | AF465816 |
| <i>Laurencia nidifica</i> J.Agarth | United States, Hawaii, Oahu, 20.V.2007, A. Sherwood (ARS02581) | GU223888 | – |
| <i>Laurencia nidifica</i> | United States, Hawaii, A. Sherwood (ARS00704) | HQ422750 | – |
| <i>Laurencia nidifica</i> | United States, Hawaii, A. Sherwood (ARS02526) | HQ423054 | – |
| <i>Laurencia nidifica</i> | United States, Hawaii, A. Sherwood (ARS02485) | HQ423048 | – |
| <i>Laurencia nidifica</i> | United States, Hawaii, A. Sherwood (ARS00687) | HQ422753 | – |
| <i>Laurencia cf. nidifica</i> | New Caledonia, Ile des Pins, 30.XI.2005, C. Payri | – | FJ785315 |
| <i>Laurencia nipponica</i> Yamada | Japan, Hokkaido, Muroran, 5.VI.2003 | GU223875 | – |
| <i>Laurencia nipponica</i> | Japan, Hokkaido, Kinaoshi, 10.V.2008 | GU223876 | – |
| <i>Laurencia obtusa</i> (Huds.) J.V.Lamour. | Ireland, County Donegal, Fanad Head, 6.VII.1998, C. Maggs | – | AF281881 |
| <i>Laurencia obtusa</i> | France, Languedoc-Roussillon, Pyrenees-Orientales, Cap Beart, Banyuls-sur-Mer, 11.VII.2007, L. Bittner | KX258828 | – |
| <i>Laurencia oliveirana</i> Yonesh. | Brazil, Rio de Janeiro, Arraial do Cabo, Ponta da Cabeça, 7.VII.2008, V. Cassano & J. De-Paula | – | JF810352 |
| <i>Laurencia pacifica</i> Kylin | United States, California, Moss Beach, Central Beach, 17.II.1992, S. Fredericq | – | AY588411 |
| <i>Laurencia pacifica</i> | United States, California, Pebble Beach, Stillwater Cove, 20.V.2010, B. Clarkston, K. Hind & S. Toews (GWS022101) | KM254466 | – |
| <i>Laurencia pacifica</i> | United States, California, Pebble Beach, Stillwater Cove, 20.V.2010, B. Clarkston, K. Hind & S. Toews (GWS022084) | HQ544189 | – |
| <i>Laurencia pumila</i> (Grunow) Papenf. | South Africa, KwaZulu-Natal, Sodwana Bay, Jesser Point, 9.VI.2010, R. Anderson & J. Bolton | – | KY927730 |
| <i>Laurencia pyramidalis</i> Bory ex Kütz. | France, Brittany, Roscoff, 5.XII.2002, F. Rousseau | – | FJ785316 |
| <i>Laurencia pyramidalis</i> | Portugal, Azores, Sao Miguel, Mosteiros, 27.VI.2011, M. Fujii, A. Prestes, A. Pacheco & M. Machin-Sanchez | KF492751 | – |

APPENDIX 1. — Continuation.

| Taxa | Voucher/ Collection data | COI-5P Accession numbers | rbcl Accession numbers |
|--|---|--------------------------------|------------------------------|
| <i>Laurencia pyramidalis</i> | Portugal, Madeira, Seixal, Praia da Laje, 7.VII.2011, E. Nogueira, V. Cassano & A. Senties | KF492733 | – |
| <i>Laurencia pyramidalis</i> | Spain, Canary Islands, Fuerteventura, Garcey, 10.IX.2012, M. Machin-Sanchez | KF492756 | – |
| <i>Laurencia pyramidalis</i> | Spain, Canary Islands, Tenerife, Puerto de La Cruz, 20.V.2011, M. Gil-Rodríguez & M. Machin-Sanchez | KF492746 | – |
| <i>Laurencia pyramidalis</i> | Spain, Canary Islands, Lanzarote, Pechiguerras, 11.IV.2012, M. Gil-Rodríguez & M. Machin-Sanchez | – | KF492791 |
| <i>Laurencia saitoi</i> Perest. | United States, California, Monterey, McAbee Beach, 21.V.2010, B. Clarkston, K. Hind & S. Toews (GWS022101) | HQ544222 | – |
| <i>Laurencia stegengae</i> C.Francis, J.J.Bolton, Mattio & R.J.Anderson | South Africa, Western Cape, Buffel's Bay, 17.IX.2008, R. Anderson & J. Bolton | – | KY927761 |
| <i>Laurencia venusta</i> Yamada | Australia, Lord Howe Island, Sylphs Hole, 26.X.2005, Y. Metti & A. Millar | – | KY120345 |
| <i>Laurencia venusta</i> | Mexico, Quintana Roo, Puerto Morelos, Punta Brava, 18.IV.2004, J. Diaz-Larrea & A. Senties | – | EF061655 |
| <i>Laurencia viridis</i> Gil-Rodríguez & Haroun | Spain, Canary Islands, Tenerife, Punta del Hidalgo, Roca Negra, 6.X.2005, M. Gil-Rodríguez | – | EF685999 |
| <i>Laurencia viridis</i> | Spain, Canary Islands, Tenerife, Punta del Hidalgo, 13.I.2012, M. Gil-Rodríguez & M. Machin-Sanchez | KF492758 | – |
| <i>Laurencia viridis</i> | Portugal, Azores, Santa Maria, Emisores, 2.VII.2011, E. Nogueira, V. Cassano & A. Senties | KF492759 | – |
| <i>Laurencia viridis</i> | Portugal, Azores, Santa Maria, Boca de Ribeira Seca, 2.VII.2011, M. Fujii, A. Neto, J. Pombo, M. Machin-Sanchez | KF492760 | – |
| <i>Laurencia viridis</i> | Portugal, Azores, Santa Maria, Boca de Ribeira Seca, 2.VII.2011, M. Fujii, A. Neto, J. Pombo, M. Machin-Sanchez | – | KF492794 |
| <i>Laurencia yamadana</i> M.Howe | United States, Hawaii, Maui, Kihei, 5.IV.2006, A. Carlile | – | GQ252550 |
| <i>Laurencia</i> sp. 1 | New Caledonia, Loyalty Is., Maré, 19.III.2005, C. Payri | KX258819 | – |
| <i>Laurencia</i> sp. 2 | New Caledonia, Lagon Sud-Ouest, Ilot Larégnère, 31.I.2008, J. Martin-Lescanne | KX258824 | – |
| <i>Laurencia</i> sp. | Oman, Dhofar, IX.2001, M. Wynne | – | KX146184 |
| <i>Laurencia</i> sp. | Sri Lanka, Odayapiti lagoon, 8.XI.2006, E. Coppejans | KX258818 | KX146176 |
| <i>Laurenciella marilzae</i> Gil-Rodríguez, Senties, Díaz-Larrea, Cassano & M.T. Fujii | Spain, Canary Islands, Tenerife, Punta del Hidalgo, 12.VII.2006, M. Gil-Rodríguez | – | EF686002 |
| <i>Laurenciella marilzae</i> | Spain, Canary Islands, Lanzarote, Pechiguerras, 15.I.2013, M. Gil-Rodríguez & M. Machin-Sanchez | KF492762 | – |
| <i>Laurenciella marilzae</i> | Portugal, Azores, Sao Miguel, Cerco da Caloura-Baia, 26.VI.2011, E. Nogueira, V. Cassano & A. Senties | KF492765 | – |
| <i>Laurenciella marilzae</i> | Spain, Canary Islands, Tenerife, Punta del Hidalgo, 13.I.2012, M. Gil-Rodríguez & M. Machin-Sanchez | KF492769 | – |
| <i>Laurenciella marilzae</i> | Italy, Palermo, Ustica Island, 4.IX.2017, D. Serio, G. Furnari & Y. Metti | – | MT822845 |
| <i>Laurenciella marilzae</i> | Italy, Sicily, Brucoli, Siracusa, 18.VII.2017, D. Serio, G. Furnari & Y. Metti | – | MT822841 |
| <i>Laurenciella mayaimii</i> Collado-Vides, Cassano & M.T.Fujii | United States, Florida, Key Largo, 14.VIII.2013, L. Collado-Vides, V. Cassano & M. Fujii | MG004178 | MG004183 |
| <i>Laurenciella mayaimii</i> | United States, Florida, Biscayne Bay, 12.VIII.2013, L. Collado-Vides, V. Cassano & M. Fujii | MG004176 | – |
| <i>Laurenciella namii</i> Popolizio, C.W.Schneid. & C.E.Lane sp. nov. | Bermuda, north shore Bermuda I., Spanish Point Park, 25.VIII.2010, C. Schneider, C. Lane & T. Popolizio; BDA 0502 [CWS/CEL 10-33-13] | OK209886 | OK209870 |
| <i>Laurenciella namii</i> sp. nov. | Bermuda, north shore Bermuda I., Spanish Point Park, 18.I.2012, C. Schneider, C. Lane & T. Popolizio; Holotype: BDA 0597 [CWS/CEL 12-11-2] | OK209887 | – |
| <i>Laurenciella namii</i> sp. nov. | United States, Florida, Key West, White Street Pier, 29.V.2013, C. Schneider, C. Lane, D. McDevit & T. Popolizio; KW 109 [CWS/CEL/TRP 13-9-5] | OK209907 | OK209871 |
| <i>Laurenciella namii</i> sp. nov. | United States, Florida, Key Biscayne, Crandon Park, 12.VIII.2013, L. Collado-Vides, V. Cassano & M. Fujii | MG004179 | MG004184 |
| <i>Laurenciella</i> sp. 2Brazil | Brazil, Espirito Santo, Anchieta, Ilhote de Ubu, 30.VI.2007, E. Stein | – | **** |
| <i>Laurenciella</i> sp. 3Brazil | Brazil, Sao Paulo, Ilha Vitoria, 19.V.2008, M. Fujii | – | **** |
| <i>Laurenciella</i> sp. 1Bda | Bermuda, Gibbet I., mouth of Flatts Inlet, 2.II.2012, T. Popolizio; BDA 0806 [TRP 12-29-16] | OK209885 | OK209869 |
| <i>Ohelopapa flexilis</i> (Setch.) F.Rousseau, Martin-Lescanne, Payri & L.Le Gall | French Polynesia, Tahiti, Tahara Reef, 24.III.2007, A. Alpham | KX258830 | KX146187 |
| <i>Osmundea blinksii</i> (Hollenb. & I.A.Abbott) K.W.Nam | United States, California, San Mateo County, Ano Nuevo, Greyhound Rock, 17.VII.1996, M. Hommersand | – | AY172575 |
| <i>Osmundea caspica</i> (Zinova & Zaberzhinskaya) Maggs & L.M.Mclvor | Azerbaijan, Sangachal Bay, 1.IX.2003 | – | KX146188 |

APPENDIX 1. — Continuation.

| Taxa | Voucher/ Collection data | COI-5P Accession numbers | rbcl Accession numbers |
|---|---|--------------------------------|------------------------------|
| <i>Osmundea hybrida</i> (DC.) K.W.Nam | France, Brittany, St. Lunaire, 20.III.1999, F. Rousseau | – | FJ785317 |
| <i>Osmundea hybrida</i> | France, Brittany, Roscoff, Finistere, 12.V.2002, F. Rousseau | KX258831 | – |
| <i>Osmundea hybrida</i> | Ireland, County Donegal, Fanad Head, 7.XI.1999, C. Maggs | – | AF281878 |
| <i>Osmundea oederi</i> (Gunnerus) G.Furnari | Ireland, Donegal County, St John's Point, 12.X.1999, C. Maggs | – | AF281880 |
| <i>Osmundea osmunda</i> (S.G.Gmel.) K.W.Nam | Ireland, County Donegal, St John's Point, 12.X.1999, C. Maggs | – | AF281877 |
| <i>Osmundea osmunda</i> | France, Brittany, Le Loup, 19.V.2011, L. Couceiro & M. Robuchon | KJ960875 | – |
| <i>Osmundea osmunda</i> | France, Brittany, Roscoff, 5.XII.2002, F. Rousseau | – | FJ785318 |
| <i>Osmundea pinnatifida</i> (Huds.) Stackh. | Ireland, Galway, Black Head, H.-G. Choi & M. Guiry | – | JX828140 |
| <i>Osmundea pinnatifida</i> | Ireland, Co. Donegal, St. John's Point, 12.X.1999, C. Maggs | – | AF281875 |
| <i>Osmundea pinnatifida</i> | Ireland, Co. Donegal, St. John's Point, 12.X.1999, C. Maggs | – | AF281876 |
| <i>Osmundea pinnatifida</i> | France, Brittany, Le Loup, 8.III.2012, L. Couceiro & M. Robuchon | KJ960886 | – |
| <i>Osmundea pinnatifida</i> | Spain, Canary Islands, Tenerife, Puerto de la Cruz, San Telmo, 7.X.2005, M. Gil-Rodriguez | – | EF686005 |
| <i>Osmundea sanctarum</i> M.T.Fujii & R.Rocha-Jorge | Brazil, Sao Paulo, Parcel do Sul, Laje de Santos Marine State Park, 19.IV.2012, R. Rocha-Jorge, M. Barros-Barreto, I. Silva & M. Fujii | – | KC012600 |
| <i>Osmundea sinicola</i> (Setch. & N.L.Gardner) K.W.Nam | United States, California, Orange County, Crescent Beach, 28.V.2002, S. Murray | – | AY588407 |
| <i>Osmundea spectabilis</i> (Postels & Rupr.) K.W.Nam | Mexico, Baja California, Punta Santo Thomas, 2.VII.1996, M. Hommersand | – | AY172574 |
| <i>Osmundea spectabilis</i> | United States, California, Pacific Grove, Bird Rock, 22.V.2010, B. Clarkston, K. Hind & S. Toews (GWS022314) | KM254469 | – |
| <i>Osmundea spectabilis</i> | United States, California, Monterey, McAbee Beach, 21.V.2010, B. Clarkston, K. Hind & S. Toews (GWS022243) | KM254320 | – |
| <i>Osmundea spectabilis</i> | United States, California, Pescadero, Pigeon Point Lighthouse, 15.V.2010, B. Clarkston & K. Hind (GWS021292) | KM254866 | – |
| <i>Osmundea spectabilis</i> | United States, California, Carmel-by-the-Sea, Soberanes Point, 17.V.2010, B. Clarkston, K. Hind & S. Toews (GWS021719) | KM254508 | – |
| <i>Osmundea spectabilis</i> | United States, California, Carmel-by-the-Sea, Soberanes Point, 17.V.2010, B. Clarkston, K. Hind & S. Toews (GWS021704) | KM254561 | – |
| <i>Osmundea spectabilis</i> | United States, California, San Diego Co., Point Loma, College of the Nazarenes, 7 Jul. 1996, M. Hommersand | – | AY172572 |
| <i>Osmundea spectabilis</i> | United States, Washington, Partridge Point, Whidbey Island, 12.VII.2011, A. Savoie & K. Hind | KU564384 | – |
| <i>Osmundea spectabilis</i> | United States, Washington, Clallam Co., 28.VIII.2012, A. Carlile & J. Waaland | – | GQ252562 |
| <i>Osmundea spectabilis</i> | United States, Alaska, Sitka, 22.VI.2005, A. Carlile & J. Waaland | – | GQ252493 |
| <i>Osmundea splendens</i> (Hollenb.) K.W.Nam | Mexico, Baja California, Bahia Colnett, 2.VII.1996, M. Hommersand | – | AY172576 |
| <i>Osmundea splendens</i> | United States, California, Santa Cruz, Four Mile, 19.V.2010, B. Clarkston, K. Hind & S. Toews (GWS021992, -998) | HQ919290 | KU564461 |
| <i>Osmundea splendens</i> | United States, California, Santa Cruz, Four Mile, 19.V.2010, B. Clarkston, K. Hind & S. Toews (GWS021984) | KM254322 | – |
| <i>Osmundea splendens</i> | United States, California, Newport, Crystal Grove, 10.XII.2012, K. Miller | – | MH911631 |
| <i>Osmundea truncata</i> (Kutz.) K.W.Nam & Maggs | Spain, Canary Islands, Tenerife, La Barranquera, 5.V.2008, M. Gil-Rodriguez, M. Fujii, V. Cassano & J. Díaz-Larrea | – | JF781523 |
| <i>Osmundea</i> sp. | Spain, Canary Islands, Gran Canarias, Punta Caldar, 2008 | – | JF781519 |
| <i>Palisada coralloopsis</i> (Mont.) Senties, M.T.Fujii & Díaz-Larrea | Mexico, Quintana Roo, Cancun, Chaac-Mol Beach, 21.VIII.2005, J. Díaz-Larrea & A. Senties | – | EF061646 |
| <i>Palisada coralloopsis</i> | Bermuda, north shore Bermuda I., Bailey's Reef, 17.VIII.2012, C. Schneider, C. Lane & T. Popolizio; BDA 1336 [CWS/CEL/TRP 12-94-2] | OK209890 | OK209865 |
| <i>Palisada cervicornis</i> (Harv.) Collado- Vides, Cassano & M.T.Fujii | United States, Florida, Key Largo, Pickles Reef, 14.VIII.2014, A. Duran | – | MG030375 |
| <i>Palisada cervicornis</i> | Bermuda, Brackish Pond Flats, inner reef, north shore (3-4 m), 17.I.2012, C. Schneider, C. Lane & T. Popolizio; BDA 0559 [CWS/CEL/TRP 12-8-16] | OK209888 | OK209863 |
| <i>Palisada crustiformans</i> (McDermid) A.R.Sherwood, A.Kurihara & K.W.Nam | United States, Hawaii, Oahu, Makapuu, 26.V.2007, A. Kurihara | – | KX146196 |
| <i>Palisada flagellifera</i> (J.Agardh) K.W.Nam | Spain, Canary Islands, Tenerife, Playa Paraiso, 12.VII.2006, M. Gil-Rodriguez, M. Fujii & A. Senties | – | EF685998 |
| <i>Palisada flagellifera</i> | Spain, Canary Islands, Tenerife, Punta del Hidalgo, 13.I.2012, M. Gil-Rodriguez & M. Machin-Sanchez | KF492772 | – |
| <i>Palisada flagellifera</i> | Bermuda, SW of North Rock BAMZ "pink sand" collecting site, 16.XI.2012, T. Popolizio; BDA 1665 [TRP 12-151-8] | OK209892 | OK209866 |

APPENDIX 1. — Continuation.

| Taxa | Voucher/ Collection data | COI-5P Accession numbers | rbcl Accession numbers |
|---|---|--------------------------------|------------------------------|
| <i>Palisada furcata</i> (Cordeiro-Marino & M.T.Fujii) Cassano & M.T.Fujii | Brazil, Praia de Tambau, Paraiba, 24.II.2004, M. Fujii | – | GU330226 |
| <i>Palisada parvipapillata</i> (C.K.Tseng) K.W.Nam | New Caledonia, l'îlot Bayes, 1.I.2001, C. Payri | KX258839 | KX146194 |
| <i>Palisada parvipapillata</i> | United States, Hawaii, Oahu, Hauula Beach Park, 18.IX.2007, A. Kurihara | GU223895 | – |
| <i>Palisada patentiramea</i> (Mont.) Cassano, Senties, Gil-Rodríguez & M.T.Fujii | Philippines, A. Lluisma | – | AF489862 |
| <i>Palisada perforata</i> (Bory) K.W.Nam | Spain, Canary Islands, Tenerife, Puerto de La Cruz, San Telmo, 14.VII.2006, M. Gil-Rodríguez, M. Fujii & A. Senties | – | EU256329 |
| <i>Palisada perforata</i> | Bermuda, Bermuda I., Gravelly Bay, 22.VIII.2012, C. Schneider, C. Lane & T. Popolizio; BDA 0314 [CWS/CEL 10-21-4] | OK209891 | OK209867 |
| <i>Palisada perforata</i> | United States, Florida, Key West, Low Key Channel, 27.V.2013, C. Schneider, C. Lane, D. McDevit & T. Popolizio; KW 016 [CWS/CEL/TRP 13-6-15] | OK209883 | OK209868 |
| <i>Palisada perforata</i> | Spain, Canary Islands, Tenerife, Punta del Hidalgo, 13.I.2012, M. Gil-Rodríguez & M. Machin-Sanchez | KF492773 | – |
| <i>Palisada perforata</i> | Venezuela, Falcon, Playa Buchuacos, 6.X.2012, G. Garcia-Soto | MH388710 | – |
| <i>Palisada cf. robusta</i> K.W.Nam | New Caledonia, Lifu, 23.III.2005, C. Payri | – | FJ785321 |
| <i>Palisada</i> sp. 1Fla | United States, Florida, Cudjoe Key, Summerland Bridge, 31.V.2013, C. Schneider, C. Lane, D. McDevit & T. Popolizio; KW 234 [CWS/CEL/TRP 13-14-17] | OK209889 | OK209864 |
| <i>Palisada</i> sp. 1 | New Caledonia, Lifou, 23.III.2005, C. Payri | KX258835 | – |
| <i>Palisada</i> sp. 2 | New Caledonia, Nouméa, 4.IV.2008, J. Martin-Lescanne | KX258837 | – |
| <i>Palisada</i> sp. | South Africa, KwaZulu-Natal, Sodwana Bay, Jesser Point, 9.IX.2010, J. Bolton, R. Anderson & C. Francis | – | KY927798 |
| <i>Yuzurua iridescens</i> (M.J.Wynne & D.L.Ballant.) Senties, M.J.Wynne, Cassano, Gil-Rodríguez & M.T.Fujii | Bermuda, Bermuda I., Southampton, West Whale Bay boiler reefs, 18.VI.2006, C. Schneider & C. Lane [CWS/CEL 06-4-8] | – | OK209858 |
| <i>Yuzurua iridescens</i> | Bermuda, Bermuda I., Southampton, West Whale Bay boiler reefs, 20.I.2012, C. Schneider, C. Lane & T. Popolizio; BDA 0707 [CWS/CEL/TRP 12-21-14] | OK209902 | – |
| <i>Yuzurua poiteaui</i> (J.V.Lamour.) Martin-Lescanne | Cuba, La Habana, Rincon de Guanabo, 29.VII.2005, J. Díaz-Larrea & A. Mallea | – | EF061650 |
| <i>Yuzurua poiteaui</i> | Bermuda, St. George's I., Ferry Reach, BIOS dock, 19.VIII.2010, C. Schneider, C. Lane & T. Popolizio; BDA 0083 [CWS/CEL 10-11-3] | OK209894 | OK209860 |
| <i>Yuzurua poiteaui</i> | United States, Florida, Key West, White Street Pier, 29.V.2013, C. Schneider, C. Lane, D. McDevit & T. Popolizio; KW 141 [CWS/CEL/TRP 13-9-33] | OK209895 | OK209861 |
| <i>Yuzurua</i> sp. 1Bda | Bermuda, Bermuda I., Southampton, West Whale Bay boiler reefs, 30.V.2012, T. Popolizio; BDA 1153 [TRP 12-69-3] | OK209893 | OK209862 |
| <i>Yuzurua</i> sp. | West Indies, Guadeloupe, 3.V.2012, Karubenthos Expedition | – | KX146198 |

APPENDIX 2. — Collection data and GenBank accession numbers for ITS sequences generated in this study.

| Taxa | Voucher/ Collection data | GenBank ITS nos. | |
|--|---|-------------------------|--|
| <i>Laurencia catarinensis</i> Cordeiro-Marino & M.T.Fujii | Bermuda, Tucker's Town, Frick's Beach, 19.VIII.2010, C. Schneider, C. Lane & T. Popolizio; BDA0013 [CWS/CEL 10-5-8] | OK209908 | |
| | Bermuda, St. George's Island, Tobacco Bay, 21.VIII.2010, C. Schneider, C. Lane & T. Popolizio; BDA0177 [CWS/CEL 10-14-25] | OK209910 | |
| | Bermuda, Gravelly Bay, 22.VIII.2010, C. Schneider, C. Lane & T. Popolizio; BDA0318 [CWS/CEL 10-21-7] | OK209909 | |
| | Bermuda, north shore Bermuda I., Spanish Point Park, 25.VIII.2010, C. Schneider, C. Lane & T. Popolizio; BDA0507 [CWS/CEL 10-33-18] | OK209912 | |
| | Bermuda, south shore Bermuda I., Horseshoe Bay grotto, 20.I.2012, C. Schneider, C. Lane & T. Popolizio; BDA0678 [CWS/CEL/TRP 12-20-5] | OK209913 | |
| | Bermuda, south shore Bermuda I., Warwick Long Bay, 10.VI.2012, T. Popolizio; BDA1168 [TRP/CWS 12-71-3] | OK209911 | |
| | Bermuda, St. George's I., Whalebone Bay, 21.VIII.2010, C. Schneider, C. Lane & T. Popolizio; BDA0225 [CWS/CEL 10-16-11] | OK209918 | |
| | Bermuda, Harrington Sound, Tucker's Bay, 24.VIII.2010, C. Schneider, C. Lane & T. Popolizio; BDA0430 [CWS/CEL 10-28-1] | OK209914 | |
| | Bermuda, north shore Bermuda I., Spanish Point Park, 25.VIII.2010, C. Schneider, C. Lane & T. Popolizio; BDA0510 [CWS/CEL 10-33-24] | OK209915 | |
| | Bermuda, north shore Bermuda I., Spanish Point Park, 25.VIII.2010, C. Schneider, C. Lane & T. Popolizio; BDA0511 [CWS/CEL 10-33-23] | OK209916 | |
| <i>Laurencia dendroidea</i> J.Agardh | Bermuda, south shore Bermuda I., Horseshoe Bay grotto, 20.I.2012, C. Schneider, C. Lane & T. Popolizio; BDA0676 [CWS/CEL/TRP 12-20-4] | OK209919 | |
| | Bermuda, south shore Bermuda I., Grape Bay Beach, 7.II.2012, T. Popolizio; BDA0817 [TRP/CWS 12-30-10] | OK209917 | |
| | Bermuda, south shore Bermuda I., Capt. Williams' Bay, 15.I.2012, C. Schneider, C. Lane & T. Popolizio; BDA0523 [CWS/CEL/TRP 12-2-2] | OK209922 | |
| | Bermuda, Spanish Point Park, 18.I.2012, C. Schneider, C. Lane & T. Popolizio; BDA0599 [CWS/CEL/TRP 12-11-3] | OK209923 | |
| | Bermuda, south shore Bermuda I., Cox's Bay, Ariel Sands, 31.I.2012, T. Popolizio; BDA0769 [TRP/CWS 12-27-9] | OK209924 | |
| | Bermuda, north shore Bermuda I., Shelly Bay, Bowen Point, 15.II.2012, T. Popolizio; BDA0855 [TRP/CWS 12-33-5] | OK209921 | |
| | US Virgin Islands, St. Croix, Turtle Deli Beach, 20.XI.2013, C. Lane, T. Popolizio & E. Salomaki; STX079 [CEL/TRP 13-26-2] | OK209925 | |
| | US Virgin Islands, St. Croix, Split Bay, 22.XI.2013, C. Lane, T. Popolizio & E. Salomaki; STX150 [CEL/TRP 13-32-1] | OK209920 | |
| | <i>Laurencia microcladia</i> Kützting | | |
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