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MOLECULAR AND MORPHOLOGICAL ANALYSES REVEAL NEW TAXA ADDITIONS TO THE TRIBE STREBLOCLADIEAE (RHODOMELACEAE, RHODOPHYTA)[1]

Danilo E. Bustamante

Instituto de Investigación para el Desarrollo Sustentable de Ceja de Selva, INDES-CES, Universidad Nacional Toribio Rodríguez de Mendoza, Amazonas 01001, Peru

Department of Life Science, Chosun University, Gwangju 61452, Korea

Boo Yeon Won

Department of Life Science, Chosun University, Gwangju 61452, Korea

Michael J. Wynne

Department of Ecology and Evolutionary Biology, University of Michigan Herbarium, Ann Arbor, Michigan 48108, USA

and Tae Oh Cho[2]

Department of Life Science, Chosun University, Gwangju 61452, Korea

The recent segregation of 12 genera in the tribe Streblocladieae suggests that the taxonomy of some species belonging to *Polysiphonia* sensu lato is updated with the transfer and the proposal of new combinations. Accordingly, six new additions to the tribe Streblocladieae on the basis of morphological and molecular analyses are presented as a consequence of this new segregation. These additions include the description of the new species *Carradoriella platensis* sp. nov., the proposal of the following new combinations *Eutrichosiphonia paniculata* comb. nov., *E. tapinocarpa* comb. nov., and the reinstatement of *Vertebrata curta*, *V. decipiens*, and *V. patersonis*. Additionally, our morphological observations identified additional diagnostic features for two genera of the Streblocladieae. *Carradoriella* has branches with sexual reproductive structures arranged adaxially on branchlets, and the recently described *Eutrichosiphonia* has rhizoids with multicellular digitate haptera. Our study gives insights in regards to the distribution, the diagnostic features for delimiting genera morphologically, and the molecular evolutionary relationships in the Streblocladieae.

***Key index words:* *cox*1; morphology; new combinations; new species; phylogeny; *rbc*L; taxonomy**

***Abbreviations*: BI, Bayesian inference; BIC, Bayesian Information Criterion; *cox*1, Cytochrome c oxidase subunit 1; GTR, General Time Reversible; K2P, Kimura-2-parameter distance; MCMC, Markov chain Monte Carlo; ML, Maximum likelihood**

Initial phylogenetic analyses of *Polysiphonia* resolved this genus as comprised of three distinct and well-supported lineages: the "*Polysiphonia* group," the "*Neosiphonia* group," and the "multipericentral group" (Choi et al. 2001). The "multipericentral group" initially included species of *Boergeseniella*, *Enelittosiphonia*, and *Vertebrata*, as well as several species of *Polysiphonia* with more than four pericentral cells (Choi et al. 2001). Subsequently, the species of this group and others corresponding to *Brongniartella*, *Ctenosiphonia*, and *Pterochondria* were transferred to *Vertebrata*, the generic name with nomenclatural priority (Díaz-Tapia et al. 2017b). These species are characterized by having more than six pericentral cells per segment and multinucleate trichoblast cells (Díaz-Tapia et al. 2017b, Savoie and Saunders 2018).

A strong link between the tribes Streblocladieae and Polysiphonieae was initially demonstrated by Phillips (2001) based on 18SrRNA gene sequences. This relationship was recently confirmed, and the Streblocladieae was segregated after restricting the Polysiphonieae to include species of the lineage corresponding to *Polysiphonia* sensu stricto (Díaz-Tapia et al. 2017a, Savoie and Saunders 2018). Streblocladieae accommodates 103 species in the following 12 genera: *Acanthosiphonia*, *Aiolocolax*, *Carradoriella*, *Eutrichosiphonia*, *Kapraunia*, *Lampisiphonia*, *Leptosiphonia*, *Melanothamnus*, *Savoiea*, *Streblocladia*, *Tolypiocladia*, and *Vertebrata* (Guiry and Guiry 2020). Although these genera share the synapomorphic feature of the tribe Streblocladieae of rhizoids being cut off from the midproximal end of the pericentral cells, they lack consistent and diagnostic features to distinguish them, except for the three-celled carpogonial branch observed in *Melanothamnus* (Kim and

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[2]Author for correspondence: e-mail tocho@chosun.ac.kr.
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Lee 1999 as *Neosiphonia*) and the multinucleate trichoblast cells present in *Vertebrata* (Díaz-Tapia et al. 2017a). Accordingly, molecular phylogenetic analyses were pivotal for supporting the assignment of these 10 genera and resolving the ongoing confusion in *Polysiphonia* sensu lato (Savoie and Saunders 2018).

Traditionally, over 200 species have been reported in *Polysiphonia* sensu lato (Bustamante et al. 2017, Guiry and Guiry 2020). The recent delineation of the tribes Polysiphonieae and Streblocladieae suggests the taxonomy of most of these species will be updated in the future with the restriction of a small subset of species with morphological characteristics similar to the type *Polysiphonia* stricta for the Polysiphonieae and the transfer and proposal of new combinations in the genera of the Streblocladieae. However, the lack of diagnostic features to distinguish genera in the Streblocladieae might make these attempts difficult in the absence of molecular data.

Specimens were collected representing the genera *Carradoriella, Eutrichosiphonia, Kapraunia*, *Leptosiphonia*, *Lophosiphonia*, and *Vertebrata* that have in common more than 7 pericentral cells per segment and rhizoids that are cut off from pericentral cells. These specimens were collected in the vicinity of their type localities in Argentina, Australia, Chile, Japan, Korea, Peru, UK, and USA. We reassessed the phylogenetic relationships of these specimens based on detailed anatomical observations and by analyzing *rbc*L and *cox*1 loci.

MATERIALS AND METHODS

Morphological examination and DNA amplification. A total of 56 polysiphonous specimens were collected in the vicinity of the type localities of the species they represent (See Table S1 in the Supporting Information for details). Specimens were air-dried for morphological and molecular studies and then preserved in silica gel. Preservation, morphological observations, and measuring were done according to Bustamante et al. (2014a,b). Voucher specimens were deposited in the herbarium of Chosun University (CUK), Korea. Additionally, voucher specimens from the herbaria of the University of California (UC), Muséum national d'Histoire naturelle, Paris (PC), and Royal Botanic Gardens, Victoria (MEL), were analyzed for morpho-anatomical observations.

Genomic DNA was extracted from silica gel preserved samples using the NucleoSpin Plant II Kit (Macherey-Nagel, Düren, Germany), following the manufacturer's instructions. The *rbc*L and *cox*1 genes were amplified using the polymerase chain reaction with Bioneer reagents (Bioneer, Daejon, Korea) in the following 20-μl reaction mixture: 2.5 μl DNA, 2 mM dNTP mix, 1 × reaction buffer, 0.3–0.5 pmol each forward and reverse primer, and 0.01 U TOP DNA polymerase (Bioneer). Polymerase chain reaction protocols and primers for amplification of plastid *rbc*L and mitochondrial *cox*1 followed Bustamante et al. (2015).

Phylogenetic analyses. New *rbc*L and *cox*1 sequences were deposited in EMBL/GenBank (see Table S1 for accession numbers). Additional *rbc*L and *cox*1 sequences of *Polysiphonia* sensu lato were downloaded from GenBank. Sequences obtained in this study and those from GenBank were initially aligned using the default settings of the MUSCLE algorithm and then manually corrected with MEGA7 (Kumar et al. 2016). Identical sequences were removed from the *rbc*L and *cox*1 data. Saturation of substitution tests was performed using the DAMBE7 software (Xia 2018) to evaluate *rbc*L and *cox*1 data by plotting numbers of transitions and transversions against Kimura-2-parameter distance (K2P). The phylogenies were based on the *rbc*L locus (152 sequences; 1,447 bp) and the concatenated data combining *rbc*L and *cox*1 (99 sequences, 2,111 bp; Table S1). The best-fitting nucleotide substitution model was selected using the program PartitionFinder (Lanfear et al. 2016) with two partitions for the concatenated data. The best partition strategy and model of sequence evolution were selected based on the Bayesian Information Criterion (BIC). The general time reversible nucleotide substitution model with a gamma distribution and a proportion of invariable sites (GTR + Γ + I) was selected for *rbc*L and the concatenated data. Maximum likelihood (ML) analyses were performed with the RAxML HPC-PTHREADS-AVX2 program (Stamatakis 2014) implemented in the raxmlGUI 2.0-beta.6 interface (Edler et al. 2019) using a GTRGAMMAI model and with support assessed by 1,000 rapid bootstraps. Bayesian inference (BI) was performed with MrBayes v3.2.5 software (Ronquist et al. 2012) using Metropolis coupled MCMC and the GTR + Γ model. We plotted likelihood vs. generation using the Tracer v1.6 program (Rambaut et al. 2014) to reach a likelihood plateau and set the burn-in value. The convergence of both runs was evaluated using Tracer to observe whether the runs reached an effective sample size >200. To evaluate posterior probabilities, we conducted two runs each with four chains (three hot and one cold) for 10,000,000 generations, sampling trees every 1,000 generations. A burn-in of 25% was used to avoid suboptimal trees in the final consensus tree.

RESULTS

Phylogenetic analyses. Phylogenetic trees obtained from the ML and BI analyses of the *rbc*L and concatenated data confirmed the monophyly of Streblocladieae (Figs. 1 and 2). Our *rbc*L and multilocus phylogenies resolved the following six new additions to the Streblocladieae: *Carradoriella* sp., *Diplocladia patersonis*, *Polysiphonia curta*, *P. decipiens*, *P. paniculata*, and *P. tapinocarpa* (Figs. 1 and 2). These new additions are distributed in the genera *Carradoriella* (1 species), *Eutrichosiphonia* (2 species), and *Vertebrata* (3 species). *Carradoriella* sp. was resolved as sister to *C. virgata* in both phylogenies, diverging 1.8% in the *rbc*L gene. Three of the studied species were in the *Vertebrata* clade. *Diplocladia patersonis* and *V. ericoides* were in a sister relationship in both phylogenies and differed by 5.5% for *rbc*L. *Polysiphonia curta* was sister to the clade composed of all *Vertebrata* species in the *rbc*L locus but only sister without support to four *Vertebrata* species in the concatenated tree. *Polysiphonia decipiens* was sister to *V. aterrima* in both phylogenies differing by 4.5% for *rbc*L. Finally, two species, *P. paniculata* and *P. tapinocarpa*, were sister in both phylogenies, and these two taxa were sister to the generitype, *Eutrichosiphonia confusa*. These genetic divergence comparisons showed that these taxa are different species on the basis of

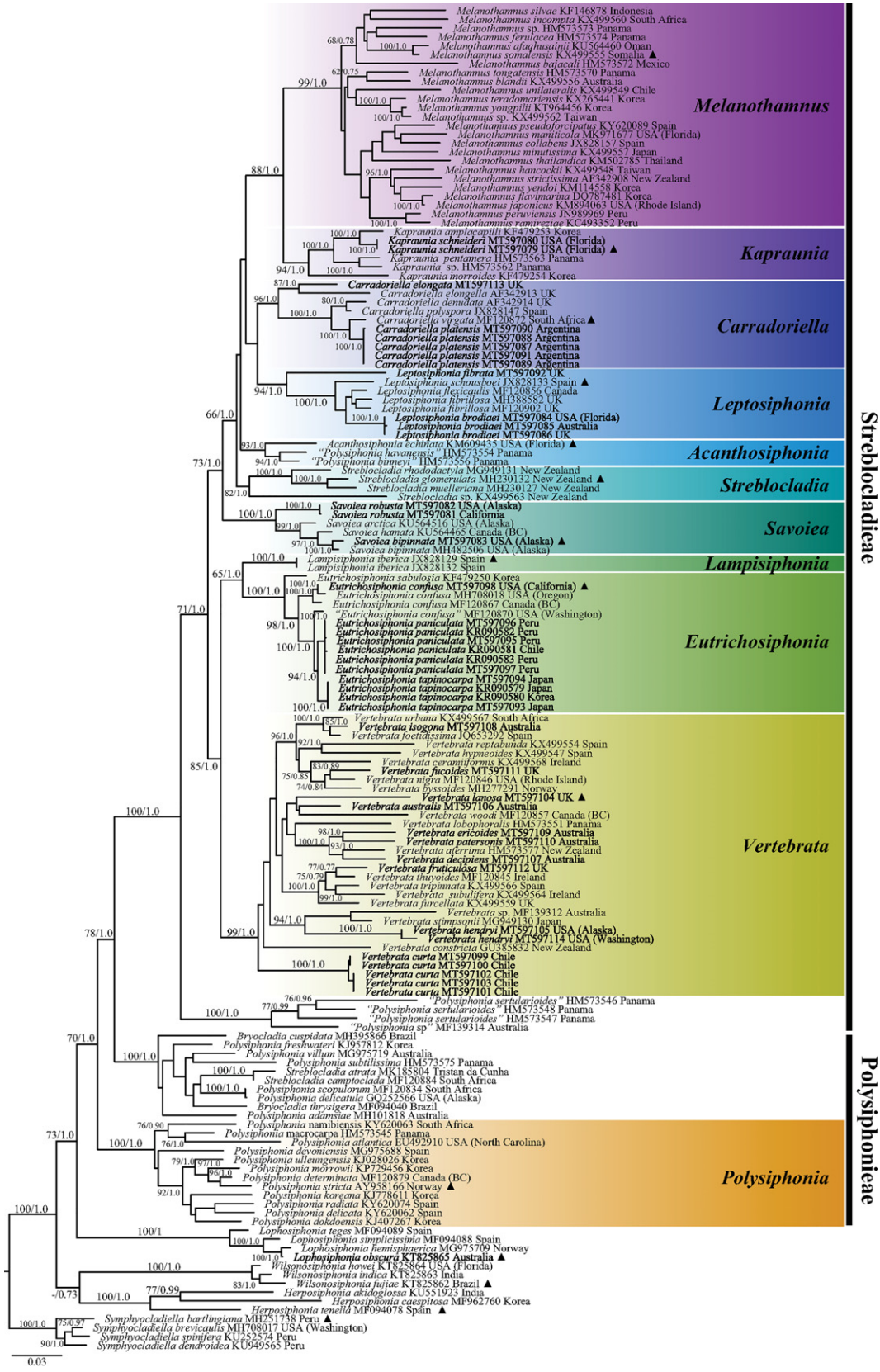

FIG. 1. Phylogenetic tree based on ML analysis of *rbc*L sequences. Values along branches are bootstrap supports and Bayesian posterior probabilities. Generitypes are indicated by ▲. Specimens from this study are shown in bold type. Scale represents nucleotide substitutions. [Colour figure can be viewed at wileyonlinelibrary.com]

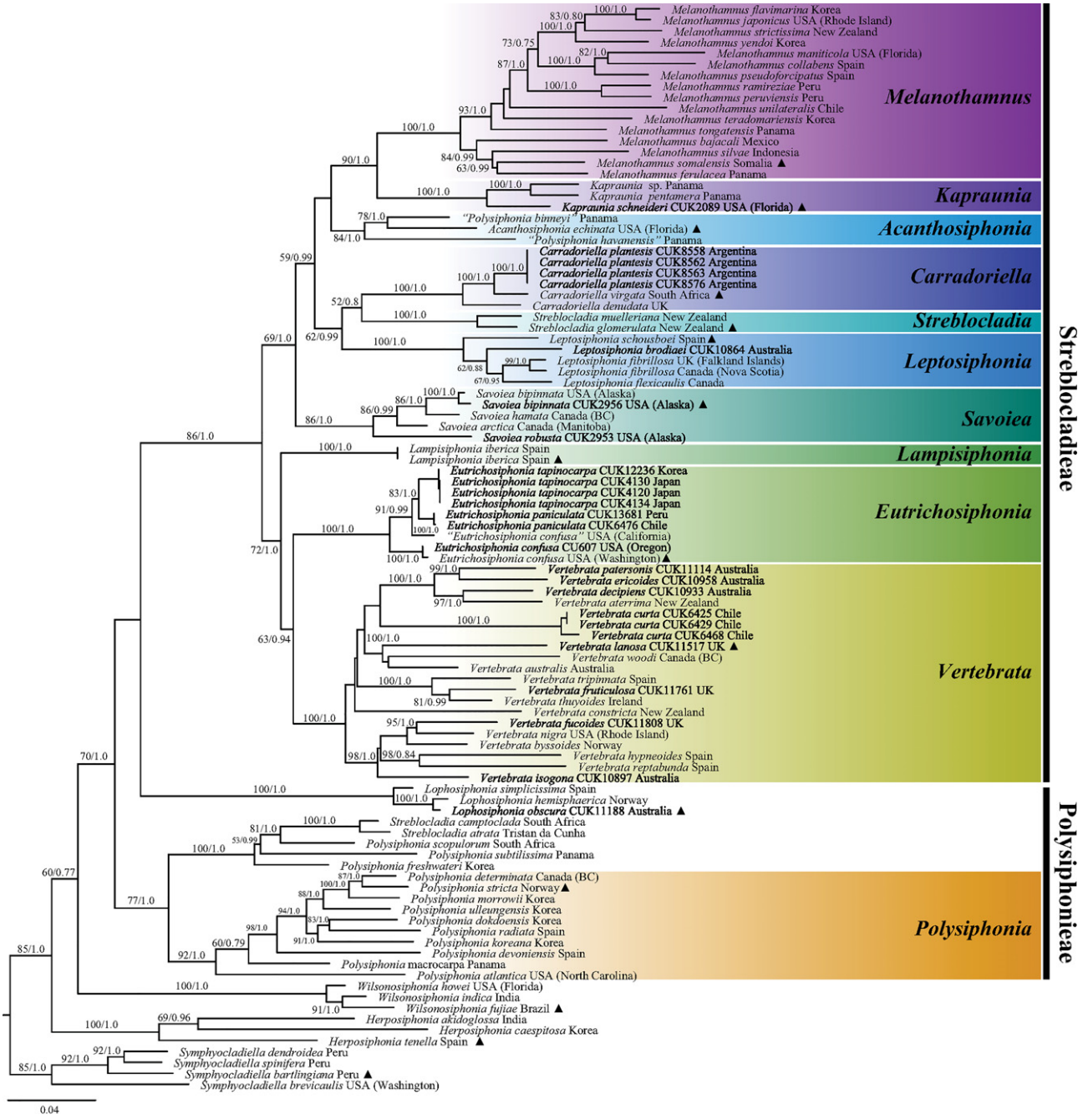

FIG. 2. Phylogenetic tree based on ML analysis of the concatenated data. Values along branches are bootstrap supports and Bayesian posterior probabilities. Generitypes are indicated by ▲. Specimens from this study are shown in bold type. Scale represents nucleotide substitutions. [Colour figure can be viewed at wileyonlinelibrary.com]

the minimum threshold (p-distance) for distinguishing species in *Polysiphonia* sensu lato (Mamoozadeh and Freshwater 2011, Bustamante et al. 2017, Savoie and Saunders 2018).

Taxonomic treatment. Additions to Carradoriella: Anatomical observations of our material identified as *Carradoriella elongata*, *C. virgata*, and *Carradoriella* sp. revealed that they share diagnostic characters, including the presence of cortication, a discoid holdfast, and cystocarps and spermatangial branches arranged adaxially on branchlets. This combination of features morphologically delineated *Carradoriella*. In addition, the unique features in *Carradoriella* sp. and its sequence differences with other congeners support the proposal of *Carradoriella* sp. as a new species:

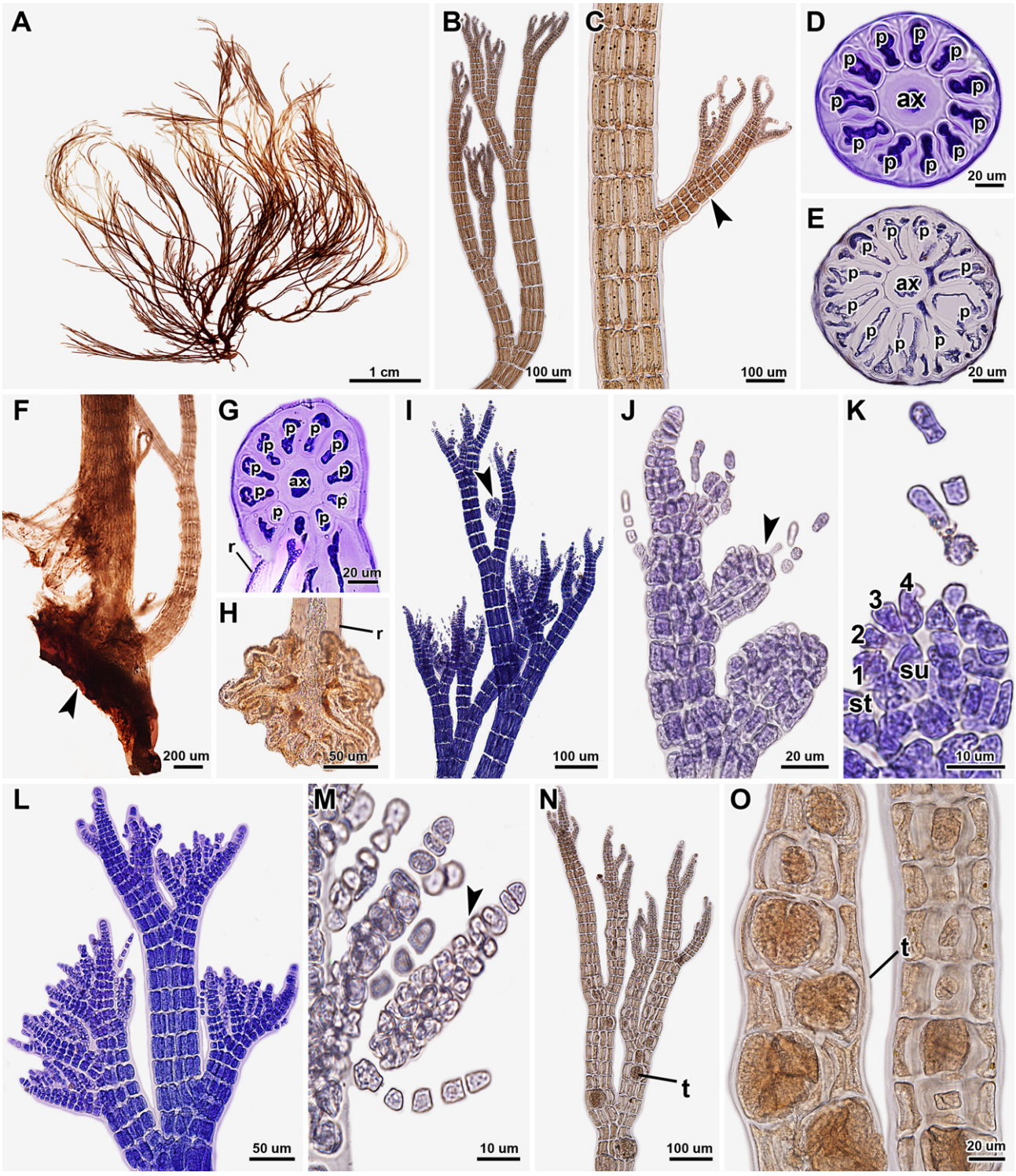

FIG. 3. Vegetative and reproductive structures of *Carradoriella platensis* sp. nov. (A) Holotype specimen (CUK 8576). (B) Erect axis showing pseudodichotomous branching pattern. (C) Erect axes showing adventitious branches. (D–E) Cross-sectional views of axes showing 10–11 pericentral cells (p) from apex (D) to basal (E) part (ax, axial cell). (F) Compact holdfast (arrowhead). G. Rhizoids (r) cutting off from pericentral cells (p) (ax, axial cell). (H) Unicellular terminations of rhizoid (r). (I–J) Procarps and cystocarps (arrowhead) along the adaxial side of the branchlets. (K) Procarp with a four-celled carpogonial branch (1–4, sequence of carpogonial branch cells; su, supporting cell; st, sterile cell). (L) Spermatangial branches along the adaxial side of the branchlets. (M) Spermatangial branch (arrowhead) arising from trichoblast. (N) Tetrasporophyte. (O) Branches showing tetrasporangia (t) arranged in spiral or straight series. [Colour figure can be viewed at wileyonlinelibrary.com]

Carradoriella platensis D.E. Bustamante, B.Y. Won & T.O. Cho, **sp. nov.** (Fig. 3).

Description. Thalli 3–12 cm tall. Branches formed replacing trichoblasts and with pseudodichotomous branching pattern. Trichoblasts scarce in vegetative thalli, but abundant in gametophytes. Adventitious branches present. Axes with 7–12 pericentral cells and dense cortication. Individual rhizoidal cells at the base of the thallus. Rhizoids cut off from the proximal end of pericentral cells with unicellular multilobed tips. Procarps composed of a supporting cell bearing a four-celled carpogonial branch. Spermatangial branches arise on a furcation of trichoblasts. Tetrasporangia arranged either in spiral or in straight series.

Holotype. CUK 8576 (Fig. 3a), July 9, 2012, leg. T.O. Cho from intertidal zone.

Type locality. Argentina, Buenos Aires, Mar del Plata, Mariano Beach, 37°58'43.11'' S, 57°32′29.85″ W.

Paratypes. CUK 8558, CUK 8563, CUK 8564, CUK 8574.

Etymology. The specific epithet "*platensis*" is derived from the locality of collection, Mar del Plata, Argentina.

Distribution. At present, known only from Argentina.

Other specimens examined. Argentina: CUK 8507, CUK 8509, CUK 8510, Puerto Madryn, Parana Beach, July, 8 2012, T.O. Cho; UC 949884 (*P. hassleri*), Patagonia, Golfo de San Matias, Puerto Antonio, W.R. Taylor.

Morpho-anatomy. Plants form large tufts predominantly attached to rock surfaces or epizoic in the intertidal zone. Thalli are 3–12 cm tall and dark red to brown. Thalli are composed of robust main erect axes attached by a prominent holdfast with a reduced or secondary prostrate system. Erect axes are distinct and form few major laterals exogenously. Erect axes are densely and radially branched in a pseudodichotomous pattern (Fig. 3, b and c) each consisting of 4-10 axial cells, rarely 20. Apical cells are prominent, 8.0 ± 1.2 μm × 9.2 ± 0.7 μm in size, and transversely divided. Trichoblasts arise on each segment near the apical cells and are delicate, deciduous, scarce in vegetative thalli but abundant in gametophytes, 1–2 times forked, 35.3 ± 11.8 μm long. After shedding trichoblasts, conspicuous scar cells are rare. Young lateral axes are pseudodichotomously and unilaterally arranged, curved in the direction of the main axes, and are composed of short segments (34.1 ± 16.4 μm). Older segments of erect axes are twisted. Near the holdfast, they are 385.1 ± 23.0 μm in diameter but after the first branch are 97.9 ± 17.1 μm in length and 150.1 ± 46.0 μm in diameter (0.7 ± 0.2 (L/D). Older segments have dense cortication and individual rhizoidal cells between pericentral cells and the axial cells. Axial segments are composed of an axial cell and 7–12 pericentral cells (Fig. 3, d and e). Adventitious branches present in basal parts (Fig. 3c). Lateral branches replace trichoblasts. Holdfasts are prominent, 634.0 ± 303.8 μm in diameter, and composed of tightly clumped rhizoids produced from basal pericentral or cortical cells (Fig. 3f). Segments of the prostrate axes are 139.0 ± 17.3 μm in length and 175.1 ± 59.4 μm in diameter (0.9 ± 0.2 L/D). Rhizoids are cut off ventrally from proximal end of the pericentral cells, 560.2 ± 262.1 μm in length, and 25.7 ± 6.2 μm in diameter with unicellular multilobed tips at maturity (Fig. 3, g and h).

In female gametophytes, erect axes are densely branched in the upper parts (Fig. 3i). Procarps are positioned in two rows in a zigzag manner along the adaxial side of the branchlets (Fig. 3j) and are composed of a supporting cell bearing a four-celled carpogonial branch and a basal sterile cell (Fig. 3k). Cystocarps are globose at maturity, 221.6 ± 39.8 μm in height and 172.1 ± 28.8 μm in diameter. In male gametophytes, spermatangial branchlets are arranged in two rows in a zigzag manner on the adaxial side of the branchlets (Fig. 3l) and are developed on the first furcation of the trichoblast (Fig. 3m). Each spermatangial branch is composed of an inner axial row of cells with surrounding spermatangial mother cells that cut off superficial spermatangia and sometimes a single sterile tip cell. In tetrasporophytes, tetrasporangia are tetrahedrally divided and 37.8 ± 8.0 μm × 39.0 ± 8.6 μm in size. Tetrasporangial branches are swollen and sinuous (Fig. 3, n and o). Tetrasporangia are arranged in spiral or straight series (Fig. 3o). Fertile pericentral cells develop a single tetrasporangium, two cover cells, and a stalk cell. A single tetrasporangium is produced in each fertile segment.

Habitat. Plants grow in the intertidal zone, forming extensive tufts. They are found attached to rocks in sheltered to wave-exposed areas. Tufts are usually wide (5 cm), long (12 cm), and very robust.

Remarks. *Carradoriella platensis* sp. nov. is distributed along the Argentinean coast from Mar del Plata to Madryn Port. It is characterized by having prominent erect main axes attached by an obvious holdfast or a reduced prostrate system, 7–12 pericentral cells per segment, heavy cortication in the basal parts of thalli, and a robust texture. These features are similar to those reported for Argentinean *Leptosiphonia brodiei* (as *P. brodiei* sensu Boraso de Zaixo 2013) and *Polysiphonia hassleri* (Taylor 1939). *Carradoriella platensis* is distinguished from authentic European material of *L. brodiei* by having cystocarps and spermatangial branches adaxially arranged. It differs from *P. hassleri* by having more than 5 pericentral cells per segment throughout based on our morphological observations of the isotype of *P. hassleri* (UC 949884). The new species is closely related to *C. virgata* in our molecular analyses (1.8% sequence divergence for *rbc*L), but *C. platensis* is distinguished by having individual rhizoidal cells and cortication restricted to basal portions of the axes.

Additions to Eutrichosiphonia. The genus *Eutrichosiphonia* was recently segregated from *Polysiphonia* by Savoie and Saunders (2018). Our morphological analyses of topotype material of *P. paniculata* from Peru and *P. tapinocarpa* from Japan as well as topotype material of the generitype *E. confusa* have revealed that these species have, as a consistent and diagnostic feature, rhizoids with multicellular terminations. The new combinations *E. paniculata* and *E. tapinocarpa* are proposed on the basis of phylogenetic analyses further supported by morphological observations.

Eutrichosiphonia paniculata (Montagne) D.E. Bustamante & T.O. Cho, **comb. nov**. (Fig. 4).

Basionym. Polysiphonia paniculata Montagne *Troisième centurie de plantes cellulaires exotiques nouvelles...*, p. 254, pl. 2, fig. 2 (1842).

Type locality. Peru "ad frondes Ulva nematoides".

Homotypic synonyms. Neosiphonia paniculata (Montagne) J.N. Norris (2014): 273. *Vertebrata paniculata* (Montagne) Kuntze (1891): 928.

Distribution. Chile and Peru.

Specimens examined. Chile: CUK 6464, CUK 6469, CUK 6476, Antofagasta, Caldera, Atacama, August 20, 2008, coll. T.O. Cho. Peru: PC 0061205-7 (Lectotype), coll. C. Gaudichaud-Beaupré; CUK 6514, CUK 6518, CUK 6523, CUK 6524, CUK 6525, CUK 6526, CUK 6540, Ica, Pisco, Lagunillas August 27, 2012, coll. T.O. Cho & D.E. Bustamante; CUK 6550, CUK 6557, Lima, Callao, August 30, 2008, coll. T.O. Cho & D.E. Bustamante; CUK 6649, Piura, Los Organos, Punta Veleros, September 04, 2008, coll. T.O. Cho & D.E. Bustamante; CUK 8233, CUK 8234, Piura, Talara, Punta Zorritos, July 02, 2012, coll. T.O. Cho & D.E. Bustamante; CUK 8251, CUK 8337, CUK 8341, CUK 8346, CUK 8361, CUK 8370, CUK 8383, CUK 8388, CUK 8393, CUK 8399, Ica, Pisco, Lagunillas, July 02, 2012, coll. T.O. Cho & D.E. Bustamante; CUK 8407, CUK 8408, CUK 8409, Lima, Callao, July 06, 2012, coll. T.O. Cho & D.E. Bustamante; CUK 13681, Lima, Callao, February 08, 2013.

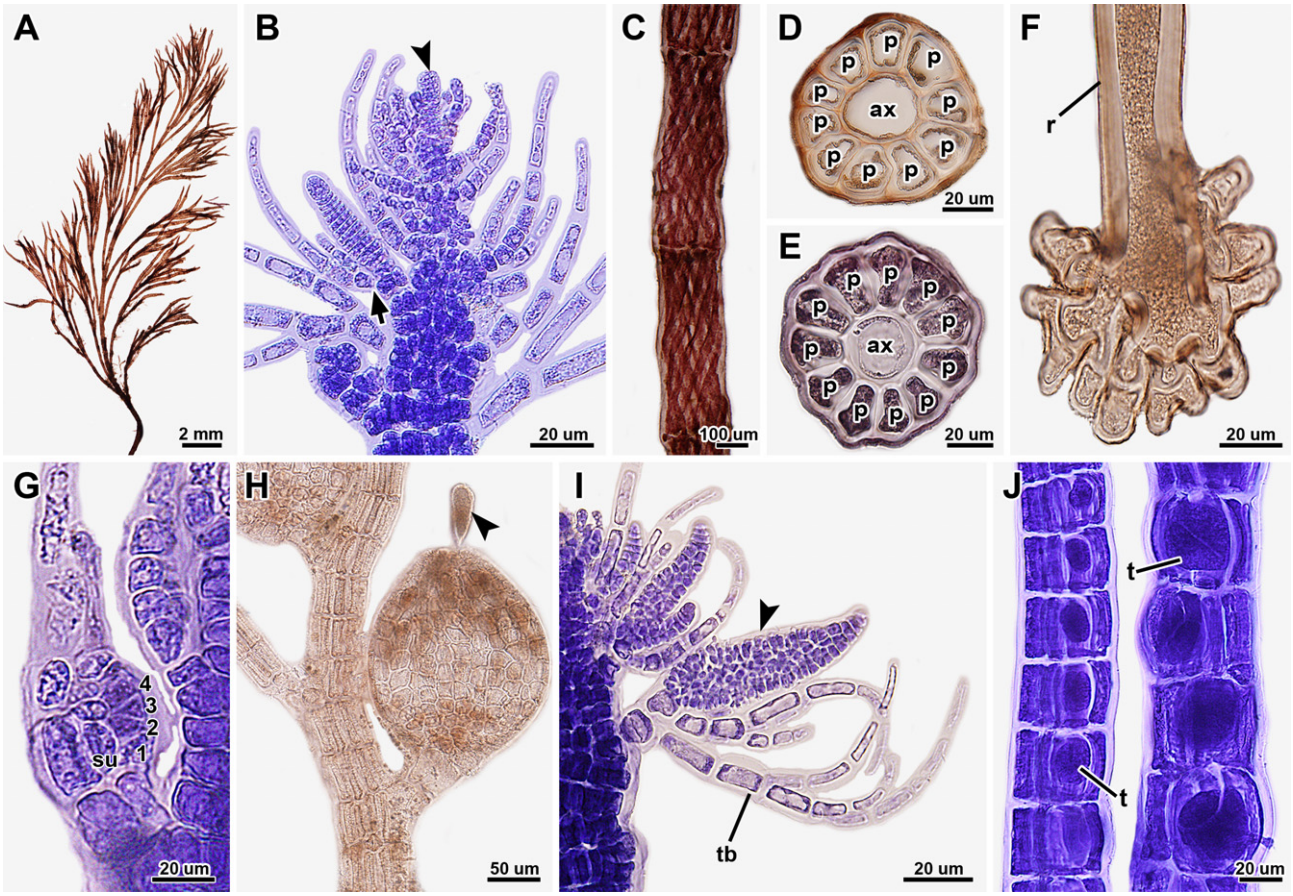

FIG. 4. Vegetative and reproductive structures of *Eutrichosiphonia paniculata* comb. nov. (A) Erect axes showing paniculate branching pattern. (B) Apex of erect axis showing prominent apical cell (arrowhead) and branch (arrow) arising in the axil of a trichoblast. (C) Axis showing long and twisted pericentral cells. (D–E) Cross-sectional views of axes showing 10–11 pericentral cells (p) from apex (D) to basal (E) part (ax, axial cell). (F) Mature rhizoid (r) with multicellular terminations. (G) Procarp with four-celled carpogonial branch (1–4, sequence of carpogonial branch cells; su, supporting cell). (H) Mature cystocarps showing globose shape; and protruded, elongate carpospore (arrowhead). (I) Spermatangial branch (arrowhead) arising from trichoblast (tb). (J) Branches showing tetrasporangia (t) arranged in spiral or straight series (t). [Colour figure can be viewed at wileyonlinelibrary.com]

Description. Plants are robust and 3–16 cm tall. Erect axes arise exogenously from the prostrate axes. They are densely and radially branched in an alternate pattern forming panicles (Fig. 4a) every 3–6 axial cells. Trichoblasts are deciduous, numerous, 1–3 times forked, arising on each segment near the apical cells (Fig. 4b). Conspicuous scar cells appear in spiral series. Pericentral cells are often spirally arranged (Fig. 4c). Each segment is ecorticate and has 9-12 pericentral cells (Fig. 4, d and e). Adventitious branches are present. Lateral branches arise in the axils of trichoblasts. Rhizoids are cut off from the center or the proximal end of the pericentral cells. Rhizoids are unicellular in younger stages but develop lobed and multicellular terminations when mature (Fig. 4f).

In female gametophytes, procarps are composed of a supporting cell bearing a four-celled carpogonial branch and a basal sterile cell (Fig. 4g). Cystocarps are alternately arranged and globose when mature (Fig. 4h). In male gametophytes, spermatangial branchlets develop on the first furcation of trichoblasts (Fig. 4i). In tetrasporangial plants, the development of tetrasporangia follows a straight or spiral arrangement (Fig. 4j). A single tetrasporangium is produced on each fertile segment.

Habitat. Plants grow from the intertidal to subtidal zone, forming extensive tufts. They are found attached to rocks in sheltered to wave-exposed areas. Tufts are usually wide (10 cm), long (16 cm), and robust and are associated in the habitat with other species such as *Centroceras clavulatum*, *Chondracanthus chamissoi*, and *Melanothamnus japonicus*.

Remarks. *Eutrichosiphonia paniculata* was originally described as *Polysiphonia paniculata* by Montagne (1842) on the basis of C. Gaudichaud-Beaupré collections (PC 0061205-7). *Eutrichosiphonia paniculata* (as *P. paniculata*) was transferred to *Neosiphonia* sect. *multisiphonia* by Norris (2014). However, our molecular analyses positioned it in *Eutrichosiphonia*. The incongruent position of *E. paniculata* (as *P. paniculata*) in *rbc*L and 18S trees collected from Chile and California was obtained from different species, and neither of them was the genuine *E. paniculata* (Díaz-Tapia et al., 2017b), which has been described from Peru (Fig. S1 in the Supporting Information). The distribution of this species along the Peruvian coast was confirmed by Dawson et al. (1964) based on its paniculate branching pattern and 10–16 pericentral cells. Our specimens collected from Peru and Chile agreed with those features and also match the external morphology of the type material (Fig. S1). Additional diagnostic features are proposed for *E. paniculata* to distinguish this species from other members of Streblocladieae (e.g., rhizoidal anatomy, tetrasporangia arrangement). The result of our present study confirms the distribution of the genuine *E. paniculata* from the northern coast of Peru (Piura, 5° S) to the northern coast of Chile (Antofagasta, 23° S).

Eutrichosiphonia tapinocarpa (Suringar) D.E. Bustamante & T.O. Cho, **comb. nov.** (Fig. 5).

Basionym. *Polysiphonia tapinocarpa* Suringar, *Annales Mus. Bot. Lugduno-Batavi* 3: 259 (1867).

Type locality. Japan.

Distribution. Japan and Korea.

Specimens examined. Japan: CUK 4120, CUK 4130, CUK 4131, CUK 4132, CUK 4133, CUK 4134, CUK 4135, Kyushu, Kumamoto, Minamiarao, April 18, 2008, coll. T.O. Cho. Korea: CUK 12236, Jeju-si, Aewol-eup, Gwakji, May 30, 2014, coll. T.O. Cho & D.E. Bustamante.

Description. Plants are delicate and 3–8 cm tall. Erect axes arise exogenously from the prostrate axes. They are densely and radially branched in an alternate pattern forming panicles (Fig. 5a) every 3–10 axial cells. Trichoblasts are delicate, deciduous, numerous, 1–3 times forked, and arise on each segment near the apical cells (Fig. 5b). Conspicuous scar cells appear in spiral series. Each segment is completely ecorticate and with 7–10 pericentral cells (Fig. 5, c and d). Adventitious branches are present. Lateral branches arise in the axils of trichoblasts. Rhizoids are cut off from the center or the proximal end of the pericentral cells. Rhizoids are unicellular in younger stages but develop lobed and multicellular terminations when mature (Fig. 5e).

The development of tetrasporangia follows a spiral arrangement (Fig. 5, f and g). A single tetrasporangium is produced in each fertile segment. Female and male gametophytes were not observed.

Habitat. Plants grow in the intertidal zone, forming extensive tufts. They are found attached to rocks in sheltered to wave-exposed areas. Tufts are usually broad (5 cm), long (8 cm), and delicate, and form monospecific patches of limited size.

Remarks. *Eutrichosiphonia tapinocarpa* was originally described as *Polysiphonia tapinocarpa* from Japan by Suringar (1867). It is characterized by having soft filaments, 8–10 twisted pericentral cells per segment, and abundant trichoblasts (Suringar 1867, Segi 1951). Although Suringar (1867) observed cortication in the basal axes, Segi (1951) recognized this cortication as distorted siphons near the base after reviewing the holotype (L 910.184.2612). Our specimens from Kyushu, Japan, and Jeju, Korea, correspond to the description of both Suringar and Segi, except for basal cortication. Additional diagnostic features are proposed to distinguish this species from other members of Streblocladieae (e.g., rhizoidal anatomy). In this study, we report *E. tapinocarpa* from Korea for the first time.

Additions to Vertebrata: Morphological observations of topotype material of *Diplocladia patersonis*, *Polysiphonia curta*, *P. decipiens*, *Vertebrata ericoides*, *V. fucoides*, *V. fruticulosa*, *V. hendryi*, *V. isogona*, and *V. lanosa* revealed that species of *Vertebrata* have greater than six pericentral cells per segment as a common character. The following taxa are reinstated in *Vertebrata*.

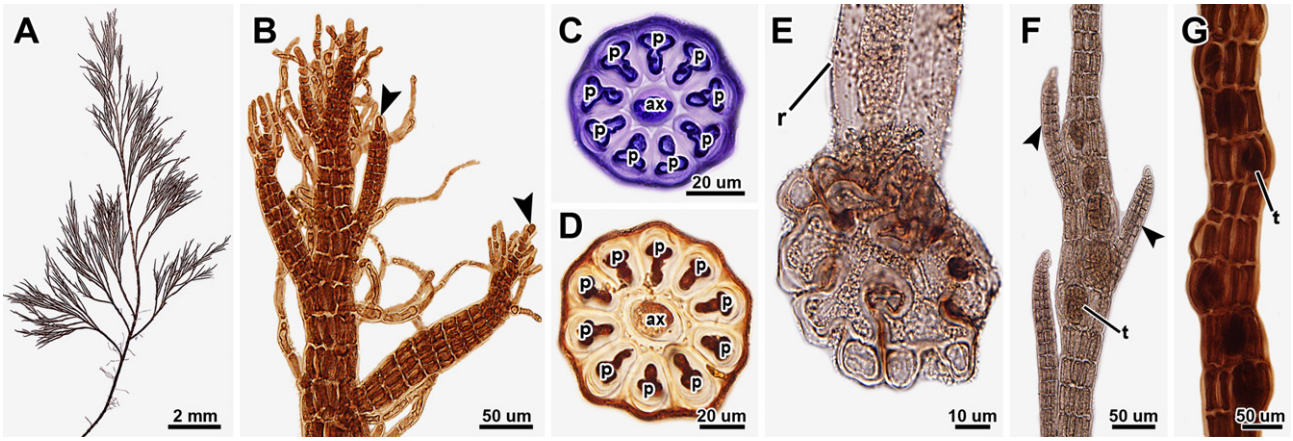

FIG. 5. Vegetative and reproductive structures of *Eutrichosiphonia tapinocarpa* comb. nov. (A) Erect axes showing paniculate branching pattern. (B) Apical region showing prominent apical cells (arrowheads) and abundant trichoblasts. (C–D) Cross-sectional views of axes showing 9–10 pericentral cells (p) from apex (C) to basal (D) part (ax, axial cell). (E) Mature rhizoids with multicellular terminations (r). (F) Upper part of tetrasporangial axes with adventitious branches (arrowheads). (G) Axis showing spiral arrangements of tetrasporangia (t). [Colour figure can be viewed at wileyonlinelibrary.com]

Vertebrata curta (Montagne) Kuntze (1891) (Fig. 6).

Basionym. *Polysiphonia curta* Montagne, *Ann. Sci. Nat., Bot. Sér. 2*, 20: 301-302. (1843).

Type locality. Peru.

Heterotypic synonym. *Polysiphonia polymorpha* Montagne *nom. illeg.* (1843): 310. This is an illegitimate name due to the binomial having been used earlier by Duby (1830).

Distribution. Endemic to the temperate Pacific coast of South America.

Specimens examined. California: UC 95208 (*P. indigena*, topotype), Santa Cruz, C.L. Anderson; UC 221279 (*P. indigena*), San Diego, F.S. Collins. Indonesia: UC 262706 (*P. curta* Montagne *sensu* Setchell); Flores, Sikka-ille, 1888, Weber van Bosse. Peru: PC 0060767 (Lectotype), UC 1883969 (Isotype), coll. D'Orbigny; Chile: CUK 6424, CUK 6425, Antofagasta, August 17, 2008, coll. T.O. Cho; CUK 6443, Antofagasta, Caleta El Bote, August 19, 2008, coll. T.O. Cho; CUK 6448, CUK 6449, Antofagasta, El lagarto Island, August 19, 2008, coll. T.O. Cho; CUK 6465, CUK 6466, CUK 6468, Antofagasta, Tocopilla, August 20, 2008, coll. T.O. Cho; CUK 6496, Valparaiso, Quintay, Playa Chica, Chile, August 22, 2008, coll. T.O. Cho; CUK 6497, CUK 6498; Valparaiso, August 23, 2008, coll. T.O. Cho.

Description. Plants are delicate and 0.6–3.5 cm tall. Erect axes arise exogenously from the prostrate axes. They are densely and radially branched in a subdichotomous and alternate pattern (Fig. 6a). Trichoblasts and scar cells are absent (Fig. 6b). Each segment is ecorticate and has 13–22 pericentral cells (Fig. 6, c and d). Adventitious branchlets are absent. Lateral branches do not arise in relation to trichoblasts. Rhizoids are cut off from the proximal end of the pericentral cells. Rhizoids are unicellular with multilobed terminations.

In female gametophytes, procarps are composed of a supporting cell bearing a four-celled

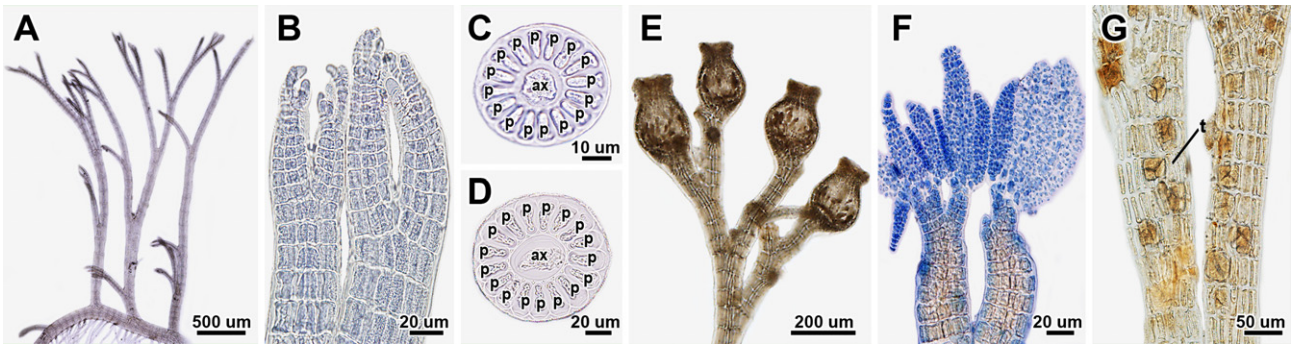

FIG. 6. Vegetative and reproductive structures of *Vertebrata curta*. (A) Plant showing pseudodichotomous branching pattern. (B) Apex lacking of trichoblasts. (C–D) Cross-sectional views of axes showing 16–17 pericentral cells (p) from apex (C) to basal (D) part (ax, axial cell). (E) Mature urceolate cystocarp. (F) Apex showing spermatangial branches clustered on the apices of erect axes. (G) Apical branches showing spiral arrangement of tetrasporangia (t). [Colour figure can be viewed at wileyonlinelibrary.com]

carpogonial branch and a basal sterile cell. Cystocarps are apically arranged and ovate to urceolate when mature (Fig. 6e). In male gametophytes, the spermatangial branchlets develop from a basal cell arising from each segment without the production of trichoblasts (Fig. 6f). In tetrasporangial plants, the development of tetrasporangia has a spiral or straight arrangement (Fig. 6g). A single tetrasporangium is produced from each fertile segment.

Habitat. Plants grow in the intertidal zone, forming extensive tufts. They are found attached to rocks or shells of *Perumytilus purpuratus* in sheltered areas. Tufts are usually reduced, short, very delicate, and grow with *Trematocarpus fragilis*.

Remarks. Vertebrata curta was originally described as *Polysiphonia curta* by Montagne (1843) after being named *P. polymorpha* Montagne (1839) on the basis of d'Orbigny collections (PC 0060767, UC 1883969). *Polysiphonia curta* was transferred to *Vertebrata* by Kuntze (1891). This species was briefly characterized by Montagne (1839) and Bustamante and Ramírez (2009) based on the small size (3–5 cm) and 15–20 pericentral cells. Our specimens agreed with those features and also match the morphology of the type material (Fig. S2 in the Supporting Information). Additionally, this species was reported from Indonesia by Silva et al. (1996) based on the identification made by Setchell of Weber van Bosse's collection (UC 262706). Our observations of this material revealed morphological differences to the type material and our specimens of *V. curta*. The Indonesian material has pseudodichotomous branches with corymbose apices, which is typical in *V. lanosa* (see Maggs and Hommersand 1993 for details). This suggests that the presence of *V. curta* in Indonesia is doubtful. *Vertebrata curta* was also reported from California by Hollenberg (1944), but the strictly dichotomous branching pattern of these materials (UC 95208, UC 221279) subsequently generated the description of the new species *P. indigena* by Hollenberg (1958). Therefore, the distribution of *V. curta* is restricted to the temperate Pacific coast of South America (Chile and Peru), and further studies are required to clarify the identity of specimens assigned to *V. curta* from Indonesia. Additionally, the apical position of procarps/cystocarps and spermatangial branches in *V. curta* is unusual in Streblocladieae or Polysiphonieae. The apical cell usually continues growth of the axis beyond the developing of the reproductive structures. However, the increase in size of procarps/cystocarps and spermatangial branches seems to interfere with the growth of the apical cell causing it to cease growth.

Vertebrata decipiens (Montagne) Kuntze (1891) (Fig. 7).

Basionym. Polysiphonia decipiens Montagne, *Prodromus generum specierumque phycearum Novarum*, p. 5. (1842).

Type locality. Auckland Island, New Zealand.

Heterotypic synonyms. Information obtained from Guiry and Guiry (2020): *Polysiphonia frutex* Harvey 1844, *P. fuscescens* Harvey 1844, *P. nigrita* Sonder 1845, *P. rytiphlaeoides* J.D. Hooker et Harvey 1845, *P. caespitula* Sonder 1855, *P. cancellata* Harvey 1844, *Vertebrata nigrita* (Sonder) Kuntze 1891.

Distribution. Australia and New Zealand.

Specimens observed. Auckland Island: PC 0060779 (Holotype), coll. J. D. d'Urville. Australia: CUK10914–1, Tasmania, Swansea, March 23, 2014, coll. T.O. Cho & D.E. Bustamante; CUK10933, Tasmania, Lagoon Beach, March 23, 2014, coll. T.O. Cho & D.E. Bustamante.

Description. Plants are robust and 3.3–11.6 cm tall. Erect axes arise exogenously from the reduced prostrate axes. They are radially branched in an irregular to alternate pattern every 5–11 axial cells (Fig. 7a). Trichoblasts are scarce, long, delicate, deciduous, 1–2 times forked, and arising on each segment near the apex (Fig. 7b). Conspicuous scar cells appear in irregular series. Cicatrigenous branches are present. Each segment is ecorticate and with 7–8 pericentral cells (Fig. 7, c and d). Adventitious branches are present. Lateral branches replace trichoblasts, and some developed a prominent hook (Fig. 7b). Rhizoids are cut off from the proximal end of the pericentral cells. Rhizoids are unicellular when mature.

In female gametophytes, procarps are composed of a supporting cell bearing a four-celled carpogonial branch and a lateral sterile cell. Cystocarps are irregularly arranged and elongate to ovoid when mature (Fig. 7e). In tetrasporangial plants, tetrasporangia develop in spiral series (Fig. 7f) with one or two produced in each fertile segment (Fig. 7, g and h). Male gametophytes were not observed.

Habitat. Plants grow as large tufts in the intertidal and subtidal zones. They are usually found as robust and solitary tufts epiphytic on brown seaweeds such as *Marginariella boryana* and *Cystophora* spp., and reds such as *Acrosorium* sp. or attached to solid surfaces (i.e., epilithic) in sheltered to wave-exposed areas.

Remarks. Vertebrata decipiens was described by Montagne (1842, as *Polysiphonia decipiens*) from Auckland Island (Fig. S3 in the Supporting Information) and then transferred to *Vertebrata* by Kuntze (1891). It was characterized by having mainly 7 or rarely 8 pericentral cells per segment (Womersley 2003) and varying in size and robustness with variation in pericentral cells diameter, length, and shape. Womersley (2003) concluded that this morphological variation is correlated with ecological conditions, and names placed in synonymy (e.g., *P. cancellata*, *P. fuscescens, P. frutex*) represent ecological forms or genetic variation at the subspecific level. The diagnostic features of *V. decipiens* are 7–8 pericentral cells per segment, prominent hooked branches, and elongate cystocarps. These features are in agreement with those of the type material (Fig. S3). *Vertebrata decipiens* is sister to *P. aterrima*, but it is

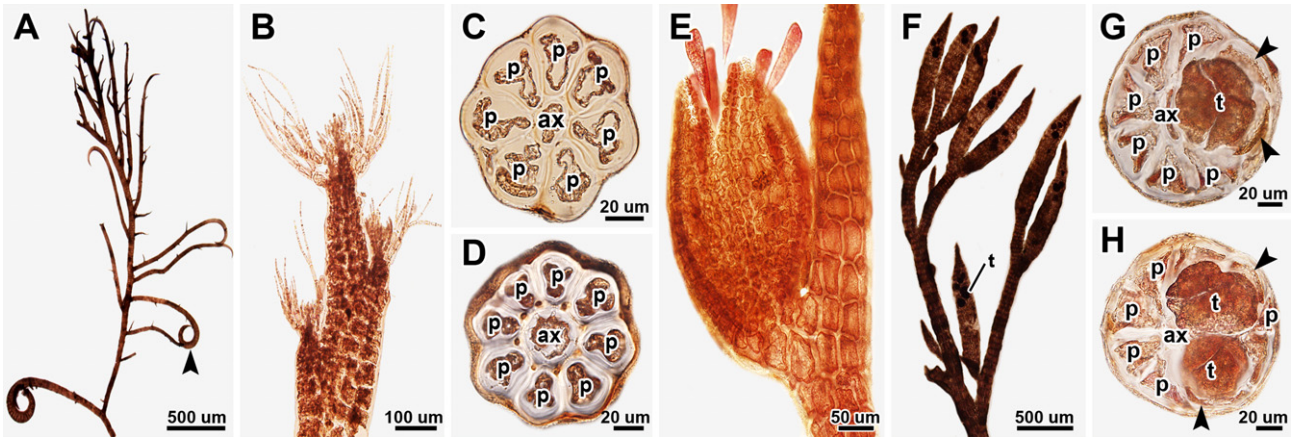

FIG. 7. Vegetative and reproductive structures of *Vertebrata decipiens*. (A) Erect axes showing the irregular branching pattern and hooked laterals (arrowhead). (B) Apex showing abundant trichoblasts. (C–D) Cross-sectional views of axes showing 7–8 pericentral cells (p) from apex (C) to basal (D) part (ax, axial cell). (E) Mature elongated cystocarp. (F) Apical branches showing spiral arrangement of tetrasporangia (t). (G–H) Cross-section views showing one (G) and two (H) tetrasporangia (t) per fertile segment rounded by cover cells (arrowheads) (p, pericentral cells). [Colour figure can be viewed at wileyonlinelibrary.com]

distinguished by its pericentral cell number and the production of one or two tetrasporangia per segment. Additionally, elongation in cystocarps of *V. decipiens* is uncommon both in Streblocladieae or Polysiphonieae, suggesting it as diagnostic feature for this species.

Vertebrata patersonis (Sonder) Kuntze (1891) (Fig. 8).

Basionym. *Polysiphonia patersonis* Sonder, *Linnaea* 26(5): 525 (1855).

Type locality. Cape Paterson, Victoria, Australia.

Homotypic synonyms. *Brongniartella patersonis* (Sonder) De Toni (1903), *Diplocladia patersonis* (Sonder) Kylin (1956).

Heterotypic synonyms. Information obtained from Guiry and Guiry (2020): *Polysiphonia spinosissima* Harvey (1859), *Brongniartella spinosissima* (Harvey) Falkenberg (1901).

Distribution. Eastern Australia.

Specimens observed. Australia: MEL 0045872 (Lectotype), Victoria, Cape Paterson, 1853, coll. F. Müller; CUK 11114, Kangaroo Island, Kingscote, Tasmania, Lagoon Beach, March 26, 2014, coll. T.O. Cho & D.E. Bustamante.

Description. Plants are delicate and 1.7–6.1 cm tall. Erect axes arise exogenously from the prostrate axes. They are radially branched in irregular pattern and covered by needle-like determinate branches (Fig. 8a). Trichoblasts are delicate, numerous, 1–2 times forked, and arise on each segment (Fig. 8b). Cicatrigenous branches are absent. Needle-like determinate branches are abundant, arising spirally

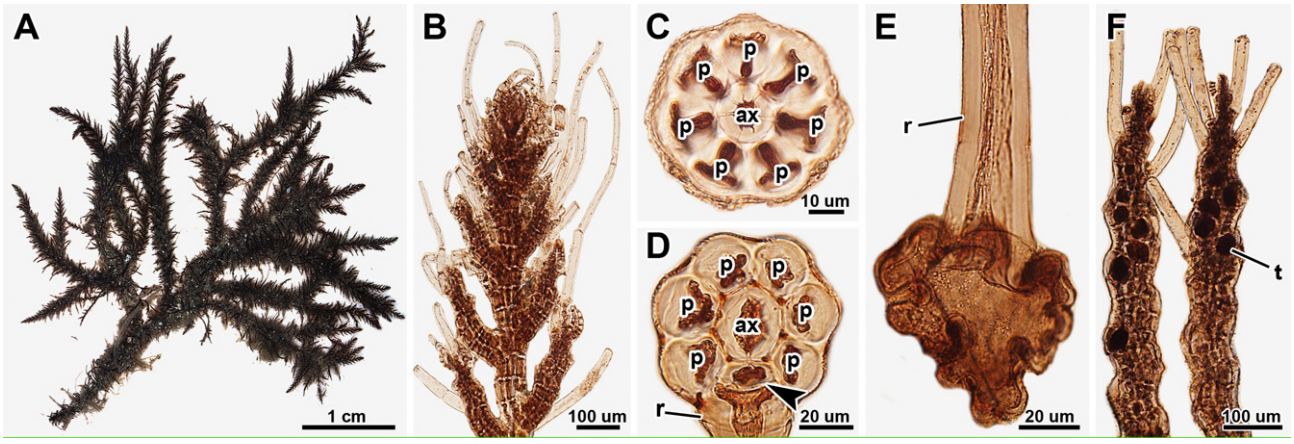

FIG. 8. Vegetative and reproductive structures of *Vertebrata patersonis*. (A) Habit showing the extended prostrate axes and erects axes. (B) Upper part of thallus showing main axes covered by young needle-like determinate branches. (C) Cross-sectional view of erect axes showing 7 pericentral cells (p) (ax, axial cell). (D) Cross-section views of prostrate axes showing rhizoids (r) cutting off from pericentral cells (arrowhead). (E) Unicellular terminations of rhizoid (r). (F) Tetrasporangial determinate branches showing spiral series of mature tetrasporangia (t). [Colour figure can be viewed at wileyonlinelibrary.com]

on the segments. Each segment is ecorticate and composed of seven pericentral cells (Fig. 8c). Adventitious branches are scarce and arise from the main filaments, but absent in the determinate branches. Rhizoids are cut off from the center or the proximal end of the pericentral cells (Fig. 8d). Rhizoids are unicellular with multilobed terminations (Fig. 8e).

Tetrasporangia form interrupted spiral series (Fig. 8f). A single tetrasporangium is produced on each fertile segment. Female and male gametophytes were not observed.

Habitat. Plants grow in the intertidal zone, forming tufts. They are attached on rocks in sheltered sites. Tufts of this species are usually very flaccid and are highly covered with epiphytes and other filamentous species.

Remarks. *Vertebrata patersonis* was originally described as *Polysiphonia patersonis* by Sonder (1855) from Victoria, Australia, on the basis of an F. Muller collection (Fig. S4 in the Supporting Information). This species is characterized by abundant spirally arranged trichoblasts (MEL 0045872), and our specimens are in agreement with those observations. *V. patersonis* (as *P. patersonis*) was transferred to *Vertebrata* by Kuntze (1891), to *Brongniartella* with a query by De Toni (1903), and later transferred to its own genus *Diplocladia* by Kylin (1956). In our phylogenetic analyses, *V. patersonis* resolved as embedded in *Vertebrata* and sister to *V. ericoides*. This finding confirmed the synonymy of *Diplocladia* under *Vertebrata*. Morphologically, the two species are distinguished by the number of pericentral cells, cortication, and trichoblast abundance. It has the following diagnostic characters: seven pericentral cells per segment, ecorticate axes throughout, and abundant spirally arranged trichoblasts (Womersley 2003). This species is restricted to the southern coast of Australia (Womersley 2003).

DISCUSSION

The six new additions to the Streblocladieae on the basis of morphological and molecular analyses are in accordance with the recent segregation of 12 genera into the tribe (Díaz-Tapia et al. 2017a, Savoie and Saunders 2018, Guiry and Guiry 2020). These additions include the description of a new species in *Carradoriella*, the proposal of two new combinations in *Eutrichosiphonia*, and the reinstatement of three species in *Vertebrata*. Additionally, our morphological observations identified diagnostic features for two genera of the Streblocladieae, namely, *Carradoriella* has branches with sexual reproductive structures arranged adaxially on branchlets, and the recently described *Eutrichosiphonia* has rhizoids with multicellular terminations.

Carradoriella was delineated with rhizoidal cells by Kylin (1956, as *Carradoria*) on the basis of *Polysiphonia virgata*. This species has been additionally placed in *Tayloriella* and *Carradoria* (Wynne 1986). However, Silva et al. (1996) proposed *Carradoriella* as a *nomen novum* for *Carradoria* Martius, a later homonym and thus an illegitimate name. *Carradoriella* was recently resurrected by Savoie and Saunders (2018) to accommodate a highly supported clade sister to *Leptosiphonia*. In our study, we found that rhizoidal cells and cortication in combination with cystocarps and spermatangial branches arranged adaxially on branchlets are consistent to delineate *Carradoriella*. *Carradoriella* appears to be restricted to the temperate Atlantic with *C. denudata*, *C. elongata*, *C. elongella*, and *P. polyspora* from the northern Atlantic, and *C. virgata* and *C. platensis* on the southwestern coast of Africa and Argentina, respectively (Maggs and Hommersand 1993, Stegenga et al. 1997).

Eutrichosiphonia was established by Savoie and Saunders (2018) to distinguish a robust molecular lineage sister to *Lampisiphonia* and *Vertebrata*. Our study shows that all the present species in the genus develop multicellular rhizoids, a character that was shown to be useful to delimit genera in Rhodomelaceae (Bustamante et al. 2017). For instance, in the tribe Herposiphoniae, *Wilsonosiphonia* was segregated from *Polysiphonia* based on the development of multicellular taproot-like rhizoids (Bustamante et al. 2017), whereas in the tribe Pterosiphonieae, the segregation of *Symphyocladiella* was supported by multicelullar rhizoids that had three- to five-celled filaments around rhizoidal tips (Bustamante et al. 2019). The multicellular lobed termination in *Eutrichosiphonia* is composed of multiple independent cells surrounding the terminations of long, tube-like rhizoids, and this pattern is unique in the tribe Streblocladieae, although rhizoids in *Lampisiphonia* occasionally become multicellular by the interpolation of an isodiametric cell at their place of origin on pericentral cells (Díaz-Tapia et al. 2017b). The anatomy of rhizoids in *Eutrichosiphonia* greatly resembles the rhizoids of *Symphyocladiella* in the tribe Pterosiphoniae (Bustamante et al. 2019). This may be an example of convergent evolution in these two phylogenetically distant lineages. *Eutrichosiphonia* seems to be restricted to the Pacific as *E. confusa* occurs in California, *E. paniculata* in Peru and Chile, *E. sabulosa* in Korea, and *E. tapinocarpa* in Japan and Korea.

Vertebrata has a world-wide distribution and is considered one of the most speciose lineages in the Streblocladieae (Díaz-Tapia et al. 2017b). Our anatomical and phylogenetic analyses of species of *Vertebrata* (e.g., *V. curta*, *V. decipiens*, *V. ericoides*, *V. fucoides*, *V. fruticulosa*, *V. hendryi*, *V. isogona*, *V. lanosa*, *V. patersonis*) confirmed that they are strongly allied molecularly despite the morphological differences between them. These taxa have as a diagnostic feature the multinucleate cells of

trichoblasts (Díaz-Tapia et al. 2017b), except for *V. lanosa*, *V. curta*, and *V. woodii* that lack trichoblasts entirely.

Molecular phylogenetic analyses were crucial for resolving evolutionary relationships of genera within the tribe Streblocladieae in the absence of diagnostic features (Savoie and Saunders 2018). However, our reassessment of species in *Carradoriella*, *Eutrichosiphonia*, and *Vertebrata* revealed that detailed anatomical observations are needed to find characters that may delineate genera. Our study provides an analysis of phylogenetic relationships in the Streblocladieae and demonstrates diagnostic features for delimiting genera. Nevertheless, further phylogenetic analyses and morphological studies, including more species, are needed to confirm the efficacy of the diagnostic characters discovered for these lineages as additional taxa presumably will be added.

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Boraso de Zaixso, A. L. 2013. *Elementos Para el Estudio de las Macroalgas de Argentina*. Universitaria de la Patagonia, Comodoro Rivadavia, 204 pp.

Bustamante, D. E. & Ramírez, M. E. 2009. El género *Polysiphonia* sensu lato en la costa norte y centro-sur de Chile (18–41°S) (Rhodophyta, Rhodomelaceae). *B. Mus. Nac. Hist. Nat.* 58:31–50.

Bustamante, D. E., Won, B. Y. & Cho, T. O. 2014a. *Polysiphonia dokdoensis* sp. nov. (Rhodomelaceae, Ceramiales) based on a population previously known as *P. atlantica sensu* Kim and Lee from Korea. *Bot. Mar.* 57:281–9.

Bustamante, D. E., Won, B. Y. & Cho, T. O. 2014b. *Polysiphonia ulleungensis* sp. nov.: a new diminutive species belonging to *Polysiphonia* sensu stricto from Korea. *Algae* 29:111–20.

Bustamante, D. E., Won, B. Y. & Cho, T. O. 2015. First record of *Neosiphonia echinata* (Rhodomelaceae, Rhodophyta) in the South Pacific: an introduced species in Southeast Asia. *Bot. Mar.* 58:345–54.

Bustamante, D. E., Won, B. Y., Miller, K. A. & Cho, T. O. 2017. A molecular phylogeny and a review of key morphological characters in *Polysiphonia* sensu lato result in *Wilsonosiphonia* gen. nov. (Rhodomelaceae, Rhodophyta). *J. Phycol.* 53: 368–80.

Bustamante, D. E., Won, B. Y., Lindstrom, S. C. & Cho, T. O. 2019. The new genus *Symphyocladiella* gen. nov. (Ceramiales, Rhodophyta) based on *S. bartlingiana* comb. nov. from the Pacific Ocean. *Phycologia* 58:9–17.

Choi, H. G., Kim, M. S., Guiry, M. D. & Saunders, G. W. 2001. Phylogenetic relationships of *Polysiphonia* (Rhodomelaceae, Rhodophyta) and its relatives based on anatomical and nuclear small-subunit rDNA sequence data. *Botany* 79:1465–76.

Dawson, E. Y., Acleto, C. & Foldvik, N. 1964. The seaweeds of Peru. *Nova Hedwigia* 13:1–111.

Díaz-Tapia, P., Maggs, C. A., West, J. A. & Verbruggen, H. 2017a. Analysis of chloroplast genomes and a supermatrix inform reclassification of the Rhodomelaceae (Rhodophyta). *J. Phycol.* 53:920–37.

Díaz-Tapia, P., McIvor, L., Freshwater, D. W., Verbruggen, H., Wynne, M. J. & Maggs, C. A. 2017b. The genera *Melanothamnus* Bornet & Falkenberg and *Vertebrata* S. F. Gray constitute well-defined clades of the red algal tribe Polysiphonieae (Rhodomelaceae, Ceramiales). *Eur. J. Phycol.* 52:1–30.

Duby, J. É. 1830. Aug. Pyrami de Candolle Botanicon gallicum sen synopsis plantarum in flora gallica descriptarum. Editio secunda. Pars secunda plantas cellulares continens. Ve Desray, Rue Hautefueille, Paris, 1068 pp.

Edler, D., Klein, J., Antonelli, A. & Silvestro, D. 2019. RaxmlGUI 2.0 beta: a graphical interface and toolkit for phylogenetic analyses using RAxML. BioRxiv 800912.

Guiry, M. D. & Guiry, G. M. 2020. AlgaeBase. World-wide electronic publication, National University of Ireland, Galway. http://www.algaebase.org; searched on 31 May 2020.

Hollenberg, G. J. 1944. An account of the species of *Polysiphonia* on the Pacific coast of North America. *II. Polysiphonia. Am. J. Bot.* 31:474–83.

Hollenberg, G. J. 1958. Phycological notes II. *Bull. Torrey Bot. Club* 85:63–9.

Kim, M. S. & Lee, I. K. 1999. *Neosiphonia flavimarina* gen. et sp. nov. with a taxonomic reassessment of the genus *Polysiphonia* (Rhodomelaceae, Rhodophyta). *Phycol. Res.* 47: 271–81.

Kumar, S., Stecher, G. & Tamura, K. 2016. MEGA7: molecular evolutionary genetics analysis version 7.0 for bigger datasets. *Mol. Biol. Evol.* 33:1870–4.

Kuntze, O. 1891. *Revisio generum plantarum*. Pars II. Arthur Felix, Dulau & Co., U. Hoepli, Gust. A. Schechert, Charles Klincksieck, Leipzig, London, Milan, New York, Paris, 1011 pp.

Kylin, H. 1956. *Die Gattungen der Rhodophyceen*. C.W.K, Gleerups, Lund, p 673.

Lanfear, R., Frandsen, P. B., Wright, A. M., Senfeld, T. & Calcott, B. 2016. PartitionFinder 2: new methods for selecting partitioned models of evolution for molecular and morphological phylogenetic analyses. *Mol. Biol. Evol.* 34:772–3.

Maggs, C. A. & Hommersand, M. H. 1993. *Seaweeds of the British Isles*. Volume 1. Rhodophyta. Part 3A. Ceramiales. HMSO, London, 444 p.

Mamoozadeh, N. R. & Freshwater, D. W. 2011. Taxonomic notes on Caribbean *Neosiphonia* and *Polysiphonia* (Ceramiales, Florideophyceae): five species from Florida, USA and Mexico. *Bot. Mar.* 54:269–92.

Montagne, C. 1839. Plantae cellulares. *In* d'Orbigny, A. [Eds.] Voyage dans 'Amérique Méridionale (le Brésil, la republique...) exécité pendant les années 1826, 1827, 1828, 1829, 1830, 1831, 1832 et 1833. Vol. 7: Botanique. Second partie. Florula Boliviensis stirpes novae et minus cognitae. Paris, pp. 1–39.

Montagne, C. 1842. Troisième centurie de plantes cellulaires exotiques nouvelles. Décades V, VI, VII et VIII. *Ann. Sci. Nat. Bot.* 18:241–82.

Montagne, C. 1843. Quatrième centurie de plantes cellulaires exotiques nouvelles. Décades VII. *Ann. Sci. Nat. Bot. Sér 2.* 20:294–306.

Norris, J. N. 2014. Marine algae of the northern gulf of California II: Rhodophyta. *Smithsonian Contribut. Bot.* 96:1–555.

Phillips, L. E. 2001. A molecular and taxonomic appraisal of selected tribes and genera of the Rhodomelaceae (Ceramiales: Rhodophyta). Ph.D. dissertation, University of Melbourne, Melbourne, 423 pp.

Rambaut, A., Suchard, M. A., Xie, D. & Drummond, A. J. 2014. Tracer v1.6, Available at: http://beast.bio.ed.ac.uk/Tracer.

Ronquist, F., Teslenko, M., Van der Mark, P., Ayres, D., Darling, A., Hohna, S., Larget, B., Liu, L., Suchard, M. A. & Huelsenbeck, J. P. 2012. MrBayes 3.2: efficient Bayesian phylogenetic inference and model choice across a large model space. *Syst. Biol.* 61:539–42.

Savoie, A. M. & Saunders, G. W. 2018. A molecular assessment of species diversity and generic boundaries in the red algal tribes Polysiphonieae and Streblocladieae (Rhodomelaceae, Rhodophyta) in Canada. *Eur. J. Phycol.* 54:1–25.

Segi, T. 1951. Systematic study of the genus *Polysiphonia* from Japan and its vicinity. *Rep. Fish. Res. Lab. Mie. Univ.* 1:167–272.
Silva, P. C., Basson, P. W. & Moe, R. L. 1996. Catalogue of the benthic marine algae of the Indian Ocean. *Univ. Calif. Publ. Bot.* 79:1–1259.
Sonder, O. G. 1855. Plantae Muellerianae. Algae annis 1852 et 1853 collectae. *Linnaea* 26:506–528.
Stamatakis, A. 2014. RAxML Version 8: A tool for phylogenetic analysis and post-analysis of large phylogenies. *Bioinformatics* 30:1312–3.
Stegenga, H., Bolton, J. J. & Anderson, R. J. 1997. *Seaweeds of the South African West Coast.* University of Cape Town, Cape Town, Bolus Herbarium, p 655.
Suringar, W. F. R. 1867. *Algarum iapoinicarum Musei botanici* L.B. index praecursorius. *Ann. Mus. Bot. Lugduno-Batavum.* 3:256–9.
Taylor, W. R. 1939. Algae collected by the "Hassler", "Albatross" and Schmitt expeditions. II. Marine algae from Uruguay, Argentina, the Falkland Islands, and the Strait of Magellan. *Pap. Mich. Acad. Sci. Arts Lett.* 24:127–64.
Womersley, H. B. S. 2003. The marine benthic flora of southern Australia, Rhodophyta, Part IIID. Ceramiales. Australian Biological Resources Study and State Herbarium of South Australia, Canberra and Adelaide, 553 pp.
Wynne, M. J. 1986. Report on a collection of benthic marine algae from the Namibian coast (southwestern Africa). *Nova Hedwigia* 43:311–55.
Xia, X. 2018. DAMBE7: New and improved tools for data analysis in molecular biology and evolution. *Mol. Biol. Evol.* 35: 1550–2.

Supporting Information

Additional Supporting Information may be found in the online version of this article at the publisher's web site:

Figure S1. Image of the Lectotype of *Polysiphonia paniculata* in PC (PC 0061205-7) collected by C. Gaudichaud-Beaupré from Peru.

Figure S2. Image of the Lectotype of *Polysiphonia curta* in PC (PC 0060767) collected by d'Orbigny from Peru.

Figure S3. Image of the Holotype of *Polysiphonia decipiens* in PC (PC 0060779) collected by J. D. d'Urville from Auckland Island.

Figure S4. Image of the Lectotype of *Polysiphonia patersonis* in MEL (MEL 0045872) collected by Müller from Australia.

Table S1. GenBank accession numbers of the cox1 and *rbc*L sequences included in the phylogenetic analysis.