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GAYLIELLA GEN. NOV. IN THE TRIBE CERAMIEAE (CERAMIACEAE, RHODOPHYTA) BASED ON MOLECULAR AND MORPHOLOGICAL EVIDENCE[1]

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On the basis of comparative morphology and phylogenetic analyses of *rbc*L and LSU rDNA sequence data, a new genus, *Gayliella* gen. nov., is proposed to accommodate the *Ceramium flaccidum* complex (*C. flaccidum*, *C. byssoideum*, *C. gracillimum* var. *byssoideum*, and *C. taylorii*), *C. fimbriatum*, and a previously undescribed species from Australia. *C. transversale* is reinstated and recognized as a distinct species. Through this study, *G. flaccida* (Kützing) comb. nov., *G. transversalis* (Collins et Hervey) comb. nov., *G. fimbriata* (Setchell et N. L. Gardner) comb. nov., *G. taylorii* comb. nov., *G. mazoyerae* sp. nov., and *G. womersleyi* sp. nov. are based on detailed comparative morphology. The species referred to as *C. flaccidum* and *C. dawsonii* from Brazil also belong to the new genus. Comparison of *Gayliella* with *Ceramium* shows that it differs from the latter by having an alternate branching pattern; three cortical initials per periaxial cell, of which the third is directed basipetally and divides horizontally; and unicellular rhizoids produced from periaxial cells. Our phylogenetic analyses of *rbc*L and LSU rDNA gene sequence data confirm that *Gayliella* gen. nov. represents a monophyletic clade distinct from most *Ceramium* species including the type species, *C. virgatum*. We also transfer *C. recticorticum* to the new genus *Gayliella*.

Key index words: **Ceramiaceae; Ceramiales; Ceramieae; *Ceramium; Gayliella* gen. nov.; LSU rDNA; morphology; phylogeny; Rhodophyta; *rbc*L; systematics; taxonomy**

Abbreviations: **Ax, axial cell; C, cortical cell; C1–4, cortical initials, numbered by sequence of formation; GC, gland cell; Cy, cystocarp; Fu, fusion cell; G, gonimoblast; Iv, involucral branchlet; P, periaxial cell; P1–7, sequence formation of periaxial cells; R, rhizoid; S, spermatangium; T, tetrasporangium.**

The tribe Ceramieae Fries (1835) currently includes 10 genera separated on the basis of thallus habit; shape, number, and arrangement of cortical cells; and the developmental morphology and arrangement of the spermatangia, carposporophyte, and tetrasporangia: (1) *Ardreanema* Norris and Abbott (1992) is characterized by three periaxial cells and a uniseriate arrangement of carposporangia forming linear gonimolobes (Norris and Abbott 1992, Abbott 1999, South and Skelton 2000); (2) *Campylaephora* J. Agardh (1851), by thick inner cortical cell layers composed of rhizoidal cells (Kylin 1956, Nakamura 1965); (3) *Carpoblepharis* Kützing (1843), by a compressed thallus and pinnate branches (Hommersand 1963); (4) *Centroceras* Kützing (1842), by spermatangia produced terminally on branched monosiphonous filaments that arise from the upper ends of the periaxial cells (Hommersand 1963); (5) *Ceramium* Roth (1797), by incomplete or complete cortication, 3–5 cortical initials per periaxial cell, and rhizoids cut off from

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periaxial and cortical cells (Cho et al. 2001a); (6) *Corallophila* Weber-van Bosse (1923), by four cortical initials produced per periaxial cell and basipetal longitudinal rows of rectangular cortical cells (Norris 1993, Cho et al. 2000); (7) *Herpochondria* Falkenberg (1897), by a prostrate habit, two lateral and four transverse periaxial cells produced per axial segment, and tetrasporangia on stichidial branches (Kylin 1956, Itono 1977); (8) *Microcladia* Greville (1830), by alternate-distichous branching, forwardly directed cortical filaments, and a continuous surface layer of relatively small, angular cells (Maggs and Hommersand 1993); (9) *Reinboldiella* G. B. De Toni (1895), by a small, repent habit and irregularly pinnate branching (Feldmann and Mazoyer 1937, Hommersand 1963); (10) *Syringocolax* Reinsche (1875), by a small, parasitic thallus arising from a basal cushion of radiating cells (Kylin 1956). Studies on various genera and species in the tribe (Hommersand 1963, Itono 1977, Womersley 1978, Maggs and Hommersand 1993, Abbott 1999, Cho et al. 2001a, Barros-Barreto et al. 2006) have helped to resolve many areas of their classification.

The genus *Ceramium* has undergone several taxonomic revisions from the time of its establishment to the present. The segregations of *Reinboldiella*, *Centroceras*, and *Corallophila* are generally accepted, while those of *Acanthoceras* Kützing (1842), *Boryna* Grateloup in Bory de Saint-Vincent (1822), *Celeceras* Kützing (1849), *Ceramiella* Børgesen (1953), *Ceramothamnion* Richards (1901), *Chaetoceras* Kützing (1847), *Dictiderma* Bonnemaison (1822), *Echinoceras* Kützing (1842), *Gongroceras* Kützing (1842), *Herpoceras* Cramer (1863), *Hormoceras* Kützing (1842), *Pteroceras* Kützing (1849), and *Trichoceras* Kützing (1849) have been rejected by most taxonomists (J. Agardh 1852, Mazoyer 1938, Hommersand 1963, Womersley 1978). The taxonomy of the genus as well as the species is still confusing because its members are delicate, small, and morphologically variable (Boo and Lee 1994), and the genus is not yet satisfactorily circumscribed (Maggs et al. 2002).

Although *C. flaccidum* (Kützing) Ardissone has been regarded as a cosmopolitan species found in cold-temperate to tropical seas (Womersley 1978), its taxonomy is complicated and confusing in its nomenclatural history. The *C. flaccidum* complex is characterized by the formation of a single rhizoidal cell formed from each of the periaxial cells. Currently, five synonyms of *C. flaccidum* (Silva et al. 1996) are recognized: *Hormoceras flaccidum* Kützing (1862) based on material from County Clare, Ireland; *C. byssoideum* Harvey (1853) based on material from Key West, Florida; *C. transversale* Collins and Hervey (1917) based on material from Spanish Rock, Bermuda; *C. masonii* Dawson (1950) and *C. taylorii* Dawson (1950) both from southern Baja California, Mexico; and *C. dawsonii* Joly (1957) from Brazil. The oldest name, *C. byssoideum,* is not available (Silva et al. 1996, pp. 919–20). *Ceramium gracillimum* (Kützing) Griffiths et Harvey var. *byssoideum* sensu Mazoyer (1938) based on material from the Mediterranean Sea is not a synonym. The detailed morphology of *C. flaccidum* was investigated by Womersley (1978) and Maggs and Hommersand (1993).

The goal of the present study was to infer the phylogenetic relationships and the taxonomic position of the *C. flaccidum* complex within the tribe Ceramieae on the basis of comparative morphology and from chloroplast-encoded *rbc*L and LSU rDNA gene sequence analyses. To do this, we collected *C. flaccidum* from near its type locality, Kilkee, Co. Clare, Ireland; *C. 'byssoideum'*, from Key West, Florida; *C. gracillimum* var. *byssoideum*, from Italy; and *C. taylorii*, from California. We obtained sequences of *C. dawsonii* from Brazil. We also collected *C. fimbriatum* Setchell and Gardner (1924), which Womersley (1978) had assigned to *C. flaccidum* and which was subsequently treated as a separate species by Silva et al. (1996, p. 397), and material previously determined as *C. flaccidum* from Australia and Brazil. Our study indicates that the *C. flaccidum* complex warrants the recognition of a new genus, encompassing several distinct species.

We start the Results section with the description of the new genus before presenting the morphological and molecular data in order to streamline the nomenclature.

MATERIALS AND METHODS

Morphology. Samples were collected worldwide and sorted according to morphology under a stereomicroscope. Each identified sample was preserved in 4% formalin/seawater for morphological observations. Microscopic observations for developmental morphology were made on material stained with 1% aqueous aniline blue acidified with 0.1% HCl.

DNA extraction, amplification, and sequencing. Genomic DNA was extracted using either the DNeasy Plant Mini Kit (QIAGEN, Valencia, CA, USA) on fresh or silica-gel dried specimens, or using a hexadecyltrimethylammonium bromide (CTAB) method (Doyle and Doyle 1987) as described in Cho et al. (2003a).

The *rbc*L gene was amplified with the primer combinations F7-R753 and F645-RrbcSstart, as listed in Lin et al. (2001), and sequenced with the primers F7, F645, F993, R376, R753, R1150, RrbcSstart (Freshwater and Rueness 1994, Lin et al. 2001, Gavio and Fredericq 2002, Cho et al. 2005). Partial fragments of LSU rDNA were amplified using the X and 28F primers (Freshwater et al. 1999). PCR and sequencing protocols were as described in Cho et al. (2003b). Sequences were determined for both forward and reverse strands using the ABI Prism 3100 Genetic Analyzer (PE Applied Biosystems, Foster City, CA, USA) with the ABI Prism BigDye™ Terminator Cycle Sequencing Ready Reaction Kit (PE Applied Biosystems).

Alignment and phylogenetic analyses. Representatives of several genera of the Ceramieae were included in the data set. Certain *Antithamnion* and *Scagelia* species were selected as the outgroup in the analyses because the tribe Antithamnieae is the sister group of the Ceramiaeae in global analyses (data not shown). Generated *rbc*L and LSU rDNA sequence data were compiled (Table S1 in the supplementary material), and the sequences were manually aligned with Sequencher (Gene Codes Corp., Ann Arbor, MI, USA). Phylogenetic analyses of *rbc*L were generated from a total of 39 new sequences, including 18

sequences from GenBank (Table S1), and conducted using the maximum-parsimony (MP) algorithm available in PAUP* (v. 4.0b10, Swofford 2003) and MrBayes v. 3.1. (Huelsenbeck and Ronquist 2001). For the MP analyses, the informative characters were excluded, and the support for nodes was determined by calculating bootstrap proportion values (Felsenstein 1985) using 1,000 bootstrap replicates (100 random additions). We used Modeltest 3.7 (Posada and Crandall 1998) to determine the simplest and most appropriate evolutionary model for our data sets. The model of nucleotide substitution selected was GTR + I + Γ, which assumes a general-time-reversible (GTR) model of sequence evolution with invariable sites (I) and a Γ distribution. For Bayesian inference, the selected model with six Markov chains was used, and 10^6 generations were run with sampling every 100 generations. Log-likelihood values stabilized around 300 generations.

Phylogenetic analyses of LSU rDNA were generated from a total of 17 sequences. MP trees were constructed with the heuristic search option of PAUP* as described above (data not shown). For the maximum-likelihood (ML) analyses, the aligned sequences were first analyzed using Modeltest (v. 3.7) (Posada and Crandall 1998). The optimal model was a GTR + I + Γ. The parameters were as follows: assumed nucleotide frequencies A = 0.2058, C = 0.1949, G = 0.3130, T = 0.2864; substitution rate matrix with A-C substitutions = 0.5027, A-G = 1.6054, A-T = 1.9391, C-G = 0.7500, C-T = 3.0166, G-T = 1.0000; proportion of sites assumed to be invariable = 0.4892, and rates for variable sites assumed to follow a gamma distribution with shape parameter = 0.4641. Support for nodes of ML tree was determined by calculating bootstrap proportion values using 100 replicates. For the MP analyses, the informative characters were excluded, and the support for nodes was determined by calculating bootstrapping proportion values (Felsenstein 1985) using 1,000 bootstrap replicates (500 random additions).

RESULTS

Gayliella T. O. Cho, L. McIvor et S. M. Boo, gen. nov.

Thalli epiphytici, pro parte prostrati, pro parte erecti, affixi ad hospitem per rhizoidea brevia, ramosi alternatim, corticati solum ad nodos; apices forcipulati; fila corticata 3–4 numerata; initium corticalis basipetalis 1-numerata, formata per divisionem horizontalem; rhizoidea unicellularia, apice digitato, formata cellulis periaxialus; cystocarpia prope apices, circumcincta involucralibus ramis; tetrasporangium formatum solum cellula periaxiali, verticillis; antheridia formata cellulis corticalibus.

Thalli epiphytic, partly prostrate and partly erect, attached to host by short rhizoidal cells, alternately branched, corticated only at the nodes; apices forcipulate; periaxial cells 4–9; 3–4 corticating filaments produced per periaxial cell; basipetal cortical initial single, produced by horizontal division; rhizoids elongate, unicellular, terminating in digitate tip, produced from periaxial cells; cystocarps near the apices, surrounded by involucral branches; single tetrasporangium produced only from periaxial cell; antheridia produced from cortical cells.

Etymology: Named in honor of Dr. Gayle I. Hansen, prominent phycologist and specialist in the taxonomy and floristics of northwest Pacific algae.

Type species: *G. flaccida* (Kützing) T. O. Cho et L. McIvor, comb. nov.

Gayliella flaccida (Kützing) T. O. Cho et L. McIvor, comb. nov. (Fig. 1, a–r).

Type locality: Kilkee, County Clare, Ireland.

Lectotype: L 940.265.55.

Syntypes: L, BM, TCD (Womersley 1978, Maggs and Hommersand 1993).

Basionym: Hormoceras flaccidum Kützing 1862: 21, pl. 69: figs. a–d.

Synonym: C. flaccidum (Kützing) Ardissone 1871: 40.

Representative specimens examined: Beau Port, Jersey, Channel Islands, English Channel (C. A. Maggs, 12.vii.1992, QUB #113, vegetative); Finavarra, Co. Clare, Ireland (C. A. Maggs, 27.ix.1992, QUB #166).

Habit and anatomy: Thalli 0.3–12 cm high, consisting of interwoven prostrate axes giving rise to erect axes (Fig. 1, a and b). Erect axes bear forcipulate, incurved, and complanate tips (Fig. 1c). Axial cells are spherical to cylindrical, reaching 84 ± 5 μm × 57 ± 5 μm [length (L) × width (W)] at the level of the seventh branching point away from the apex. Five or six periaxial cells are cut off obliquely from the upper part of each parent axial cell in an alternate sequence (Fig. 1, n–q) and remain at the nodes after axial cell elongation. The cortical bands (Fig. 1, d–g) reach 66 ± 5 μm × 99 ± 11 μm (L × W) at the seventh dichotomy away from the apex. Three cortical initials are produced from each periaxial cell in an alternate sequence and develop into corticating filaments (Fig. 1i). The first two cortical initials (C1, 2) are cut off obliquely from the anterior end of the periaxial cells (Fig. 1h) and grow acropetally (Fig. 1j); the remaining one (C3) is produced horizontally from the posterior end of the periaxial cell (Fig. 1i) and grows basipetally (Fig. 1j). At the branching point, four cortical initials are produced from a single periaxial cell in an alternate sequence: three acropetal initials and one basipetial initial (Fig. 1, l and m). The acropetal corticating filaments are 3–4 cells long, while the basipetal one is 2–3 cell long. Hairs are produced from the cortical cells (Fig. 1k).

Branches are alternately arranged and sometimes determinate (Fig. 1, a and b). Branching takes place at intervals of 7–9 (average 7.0 ± 0.9) axial cells in the main axes and at intervals of 10–14 (average 11.8 ± 1.5) axial cells in the lateral axes. Gland cells rarely develop from cortical cells of acropetally corticating filaments and are ovoid, averaging 12 ± 3 μm × 8 ± 2 μm (Fig. 1, g and j). Rhizoids are unicellular with a terminal digitate pad, and each rhizoid is produced from periaxial cells (Fig. 1r) of prostrate axes and from the lower parts of the main axes.

Reproductive thalli were not found in our collections.

Gayliella fimbriata (Setchell et N. L. Gardner). T. O. Cho et S. M. Boo, comb. nov. (Fig. 2, a–q).

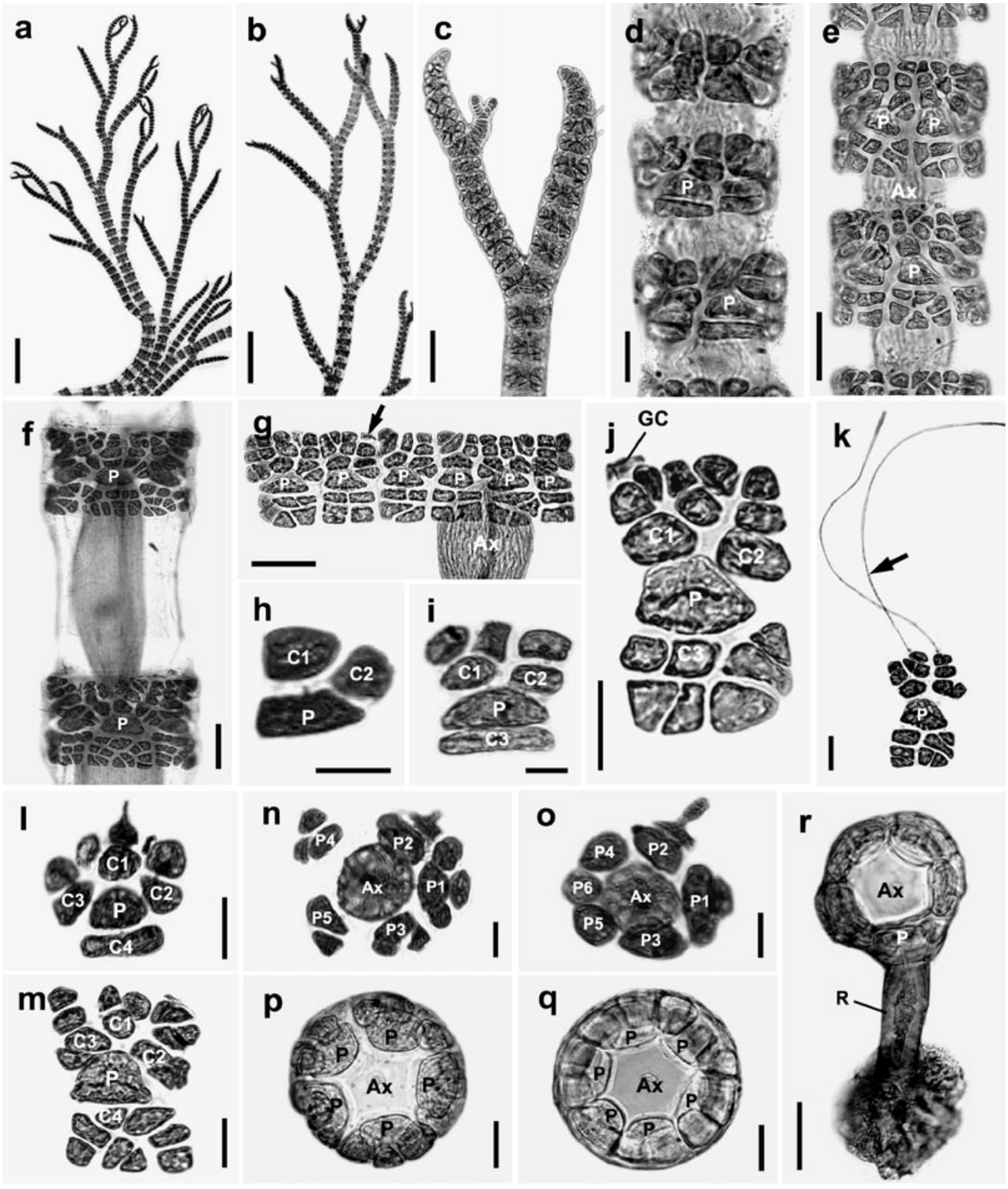

FIG. 1. *Gayliella flaccida* (Kützing) T. O. Cho et L. McIvor, comb. nov. from Beau Port, Jersey, Channel Islands, England. (a) Thallus. Scale bar, 0.5 mm. (b) Upper thallus showing alternate branching pattern. Scale bar, 0.25 mm. (c) Apical region, Scale bar, 50 μm. (d–f) Incomplete cortication in upper (d), middle (e), and lower (f) parts. Scale bars, 20 μm (d, e) and 50 μm (f). (g) Cortical node with gland cell (arrow). Scale bar, 40 μm. (h–i) Development of cortical initials showing alternate sequence of formation and horizontal division of basipetal cortical initial. Scale bars, 10 μm. (j) Mature cortication produced from a periaxial cell. Scale bar, 20 μm. (k) Mature cortication with hairs (arrow) on acropetal filaments. Scale bar, 20 μm. (l–m) Development of four cortical initials on branching point. Scale bar, 20 μm. (n–o) Cross-sectional views of young thallus showing alternate sequence formation of periaxial cells from axial cell. Scale bars, 10 μm. (p–q) Cross-sectional views through cortical nodes of mature thallus. Scale bars, 20 μm. (r) Cross-sectional view showing unicellular rhizoid with digitate tip produced from periaxial cells. Scale bar, 50 μm. Ax, axial cell; C1–4, cortical initials, numbered by sequence of formation; P, periaxial cell; P1–6, sequence formation of periaxial cells; R, rhizoid; GC, gland cell.

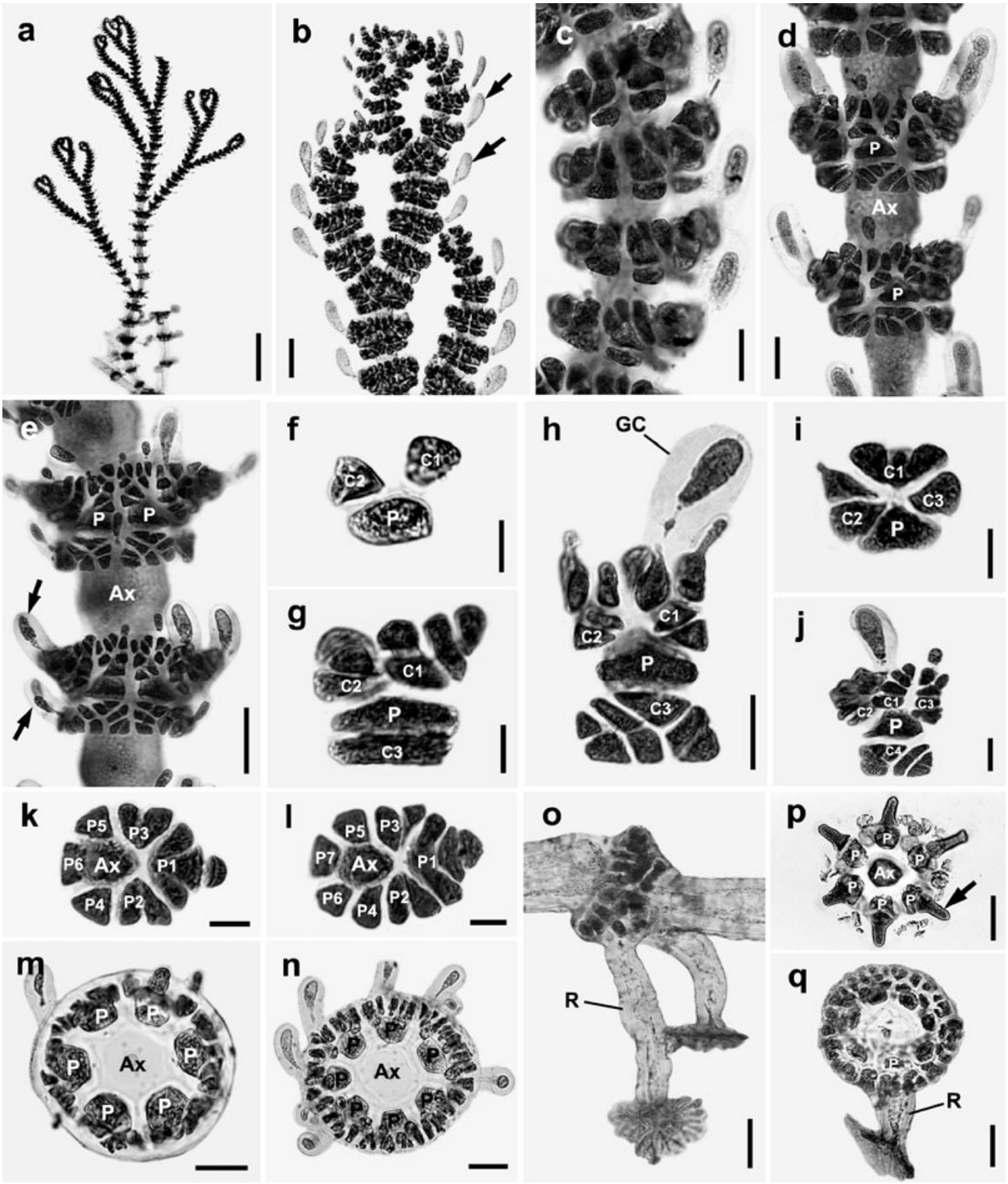

FIG. 2. *Gayliella fimbriata* (Setchell et N. L. Gardner) T. O. Cho et S. M. Boo, comb. nov. from near La Paz, Baja California. (a) Thallus. Scale bar, 0.5 mm. (b) Apical region with clavate gland cell row (arrows) on abaxial side. Scale bar, 100 μm. (c–e) Incomplete cortication showing arrangement of gland cells (arrows) produced from acropetal and basipetal cortical cells in upper (c), middle (d), and lower (e) parts. Scale bars, 20 μm (c), 50 μm (d, e). (f, g) Development of cortical initials showing alternate sequence of formation and horizontal division of basipetal cortical initial. Scale bar, 10 μm. (h) Mature cortication showing clavate gland cell from cortical filament. Scale bar, 10 μm. (i, j) Development of four cortical initials on branching point. Scale bar, 10 μm (i), 20 μm (j). (k, l) Cross-sectional views of young thallus showing alternate sequence of formation of periaxial cells from axial cell. Scale bars, 10 μm. (m, n) Cross-sectional views through cortical nodes. Scale bars, 40 μm. (o) Unicellular rhizoids with digitate tips on the creeping thallus. Scale bar, 50 μm. (p, q) Cross-sectional views showing rhizoid initials (arrow) and mature rhizoid produced from periaxial cell. Scale bars, 50 μm. Ax, axial cell; C1–4, cortical initials, numbered by sequence of formation; GC, gland cell; P, periaxial cells; P1–7, sequence formation of periaxial cells; R, rhizoid.

Type locality: Eureka, near La Paz, Baja California Sur (BCS), Mexico.

Type: Marchant nr. 87a, May, Herbarium, University of California, Berkeley (UC).

Basionym: C. fimbriatum Setchell et N. L. Gardner 1924: 777, pl. 26, figs. 43–4.

Representative specimens examined: Isla San José, BCS, Mexico (T. O. Cho and R. Riosmena-Rodriguez, 11.viii.1991, CNUK 004892-4, 004896, vegetative); Punta Perico, BCS, Mexico (T. O. Cho and R. Riosmena-Rodriguez, 05.vi.2000, CNUK 004875, 004882, vegetative).

Habit and anatomy: Thalli are 0.5–1.2 cm high, consisting of prostrate axes giving rise to erect axes (Fig. 2a). Erect axes bear forcipulate incurved and complanate apical regions (Fig. 2b). Axial cells are spherical to cylindrical, reaching 214 ± 43 μm × 89 ± 11 μm at the level of the seventh dichotomy away from the apex. Six or seven periaxial cells are cut off obliquely from the upper part of each parent axial cell (Fig. 2, k–n) and remain at the nodes after axial cell elongation. The cortical bands (Fig. 2, c–e) reach 93 ± 10 μm × 169 ± 26 μm (L × W) at the level of the seventh branching point away from the apex. Three cortical initials are produced from each periaxial cell in an alternate sequence (Fig. 2g) and develop into corticating filaments. The first two cortical initials are cut off obliquely from the anterior end of the periaxial cells and grow acropetally (Fig. 2, f and h); the remaining one is produced horizontally from the posterior end of the periaxial cell and grows basipetally (Fig. 2, g and h). At the branching point, four cortical initials are produced from a single periaxial cell in alternate sequence: three acropetal initials and one basipetal initial (Fig. 2, i and j). The acropetal corticating filaments are 3–4 cells long, while the basipetal ones are 2–3 cells long.

Branches are regularly alternate (Fig. 2a). Branching takes place at intervals of 3–5 (average 3.5 ± 0.6) axial cells in the main axes and at intervals of 4–6 (average 5.2 ± 0.7) axial cells in the lateral axes. Gland cells usually develop from cortical cells of acropetally and rarely basipetally corticating filaments (Fig. 2, e and h), becoming strongly protruding, and are clavate, averaging 59 ± 15 μm × 29 ± 6 μm (Fig. 2h). Rhizoids are unicellular with a terminal digitate pad (Fig. 2o). Each rhizoid is produced from a periaxial cell (Fig. 2, p and q) of interwoven prostrate axes and lower parts of main axes.

Reproductive thalli were not found in our collections.

Gayliella mazoyerae T. O. Cho, Fredericq et Hommersand, sp. nov. (Fig. 3, a–e).

Thalli epiphytici, partim prostrati et partim erecti; alternatim ramose corticati solum ad nodos; intervallum ramificans 4–5 ad lateralem axes 4–6; apices forcipulati, complain; periaxiales cellulae 4; glandes cellulae ovoidae; fila corticata 3-numerata per periaxiales cellulas; basipetalinum initium 1-numerata, formata per divisionem horizontalem, 1 cellulosum longum; rhizoidea elongata, unicellularia, apice digitato, formata cellulis periaxialus.

Thalli epiphytic, partly prostrate and partly erect, alternately branched, corticated only at the nodes; branching interval 4–5 for main axes, 4–6 for lateral axes; apices forcipulate, complanate; periaxial cells four; gland cells ovoid; corticating filaments 3 per periaxial cell; basipetal cortical initial single, produced by horizontal division, 1 cell long; rhizoids elongated, unicellular, terminating in digitate tip, produced from periaxial cells.

Type locality: Ognina, Catania, Sicily, Italy, 37°31′40″ N, 15°06′58″ E.

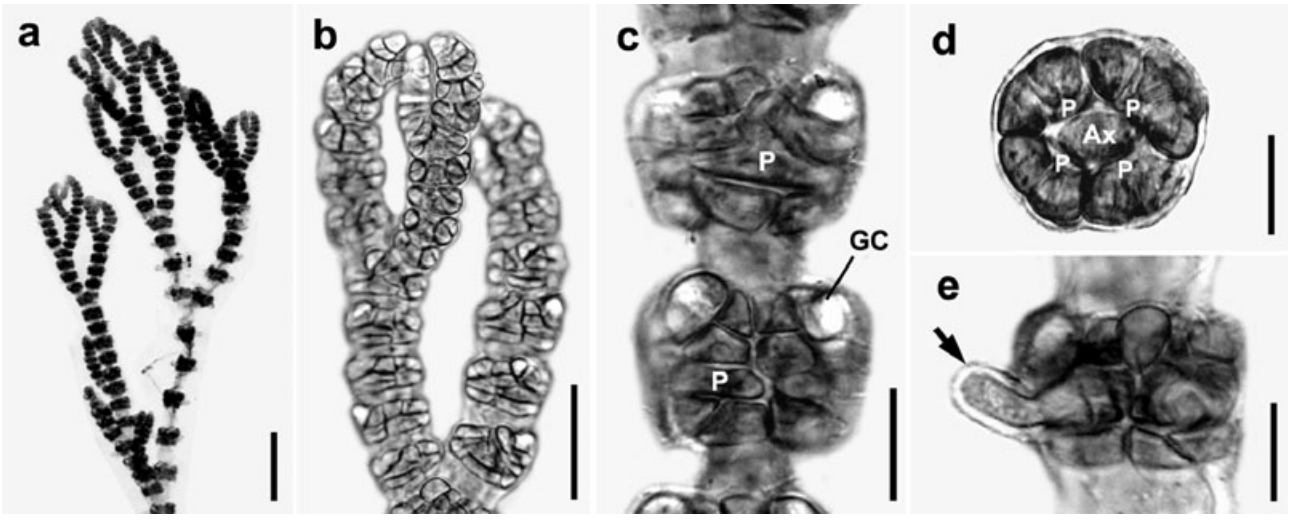

FIG. 3. *Gayliella mazoyerae* T. O. Cho, Fredericq et Hommersand, sp. nov. from Sicily, Italy. (a) Thallus. Scale bar, 0.25 mm. (b) Apical region. Scale bar, 50 μm. (c) Incomplete cortication in middle part. Scale bar, 20 μm. (d) Cross-sectional view through cortical node. Scale bar, 20 μm. (e) Unicellular rhizoid (arrow) produced from periaxial cell. Scale bar, 25 μm. Ax, axial cell; GC, gland cell; P, periaxial cell.

Holotype: CAT 164, coll. Mario Cormaci, 14.ii.1970, 5 m depth, epiphyte on *Pterocladiella capillacea*, vegetative (LAF-14.ii.70-1-1).

Isotype: CAT 164 at CAT.

Representative specimens examined: Ognina, Catania, Sicily (M. Cormaci, ii.2003, vegetative).

Taxonomic synonym: *C. gracillimum* var. *byssoideum* Mazoyer 1938: 323.

Etymology: Although *C. gracillimum* var. *byssoideum* is listed in the synonymy of *C. flaccidum*, we treat this entity as a new species, with a new name, because *C. byssoideum* is not available, being a later homonym of *Fucus byssoides* Goodenough and Woodward (1797) (Silva et al. 1996). Mazoyer (1938) made the new combination to designate Mediterranean and tropical forms of *C. gracillimum*. We call this Mediterranean plant *G. mazoyerae* in honor of Dr. Geneviève Feldmann Mazoyer and to recognize its wide distribution in the western Mediterranean and Adriatic regions.

Habit and anatomy: Thalli are to 0.9 cm high, consisting of prostrate axes giving rise to erect axes (Fig. 3a). Erect axes bear forcipulate, incurved, and complanate apical regions (Fig. 3b). Axial cells are spherical to cylindrical, reaching 80 ± 12 μm × 65 ± 8 μm at the level of the seventh branching away from the apex. Four periaxial cells are cut off obliquely from the upper part of each parent axial cell (Fig. 3d) and remain at the nodes after axial cell elongation. The cortex is incomplete and banded (Fig. 3c), the bands reaching 38 ± 3 μm × 56 ± 4 μm (L × W) in the middle thallus. Three cortical initials are produced per periaxial cell and develop into corticating filaments. The first two cortical initials are cut off obliquely from the anterior end of the periaxial cells and grow acropetally; the remaining one is produced horizontally from the posterior end. The acropetal corticating filaments are 1–2 cells long, while the basipetal one is short, 1 cell long.

Branches are regularly alternate and indeterminate (Fig. 3a). Branching takes place at intervals of 4–5 (average 4.1 ± 0.3) axial cells in the main axes and at intervals of 4–6 (average 4.9 ± 0.5) cells in the lateral axes. The lateral branches are regularly branched (Fig. 3a). Gland cells develop from cortical cells of acropetally corticating filaments and are ovoid (Fig. 3c), averaging 9.8 ± 0.7 μm × 14 ± 0.9 μm. Rhizoids are unicellular and elongate with a terminal digitate pad. Rhizoids are produced from periaxial cells of interwoven prostrate axes in the lower part of main axes (Fig. 3e).

Reproductive thalli were not found in our collections.

Gayliella taylorii (E. Y. Dawson) T. O. Cho et S. M. Boo, comb. nov. (Fig. 4, a–i).

Type locality: Cabeza Ballena, Baja California Sur, Mexico.

Type: coll. by E.Y. Dawson 3393 (AHFH 48797 in UC).

Basionym: *C. taylorii* E. Y. Dawson 1950: 127–8, pl. 2, fig. 13; pl. 4, figs. 31–33.

Representative specimens examined: Laguna Beach, Orange Co., California, USA (T. O. Cho and S. N. Murray, 03.xii.1999, CNUK 002354, 002363, 002529, vegetative); Dana Point, Orange Co., California, USA (T. O. Cho and S. N. Murray, 04.xii.1999, CNUK 002133, 002539, vegetative); Crystal Cove State Park, Orange Co., California, USA (T. O. Cho and S. N. Murray, 05.xii.1999, CNUK 002140, 002361, vegetative); Santa Catalina, California, USA (T. O. Cho and S. N. Murray, 6.xii.1999, CNUK 002482, 002484, vegetative).

Habit and anatomy: Thalli are 0.7–1.2 cm high, consisting of prostrate axes giving rise to erect axes (Fig. 4, a and b). Erect axes bear forcipulate, incurved, and complanate apical regions (Fig. 4c). Axial cells are spherical to cylindrical, reaching 97 ± 11 μm × 55 ± 9 μm at the level of the seventh dichotomy away from the apex. Six or seven periaxial cells are cut off obliquely from the upper part of each parent axial cell (Fig. 4, j and k) and remain at the nodes after axial cell elongation. The cortex is incomplete; bands (Fig. 4, d–f) reach 63 ± 2 μm × 101 ± 2 μm (L × W) at the level of the seventh branching point away from the apex. Three cortical initials are produced per periaxial cell in an alternate sequence (Fig. 4g) and develop into corticating filaments. The first two cortical initials are cut off obliquely from the anterior end of the periaxial cells and grow acropetally; the remaining one is produced horizontally from the posterior end and grows basipetally (Fig. 4, g–i). The acropetal corticating filaments are 3–4 cells long, while the basipetal one is 2–3 cells long.

Branches are regularly alternate and indeterminate (Fig. 4b). Branching takes place at intervals of 3–4 (average 3.8 ± 0.4) axial cells in the main axes and at intervals of 4–6 (average 5.3 ± 0.5) cells in the lateral axes. Gland cells develop from cortical cells of acropetally developed filaments (Fig. 4e) and are ovoid, averaging 11 ± 2 μm × 11 ± 1 μm. Rhizoids are unicellular and elongate with a terminal digitate pad. Rhizoids are produced from periaxial cells of interwoven prostrate axes in the lower part of main axes (Fig. 4, a and l).

Reproductive thalli were not found in our collections.

Gayliella transversalis (Collins et Hervey) T. O. Cho et Fredericq, comb. nov. (Figs. 5, a–n; 6, a–e).

Type locality: Spanish Rock, Bermuda.

Type: A. B. Hervey (Collins 8107, 10.iv, 1914, in NY).

Basionym: *C. transversale* Collins et Hervey 1917:145, pl. V, figs. 29–31.

Synonym: *C. byssoideum* Harvey 1853: 218, non-*C. byssoides* (Goodenough et Woodward) Ducluzeau (1806: 66). The name *C. byssoideum* Harvey, based on material from Key West, Florida, is not available

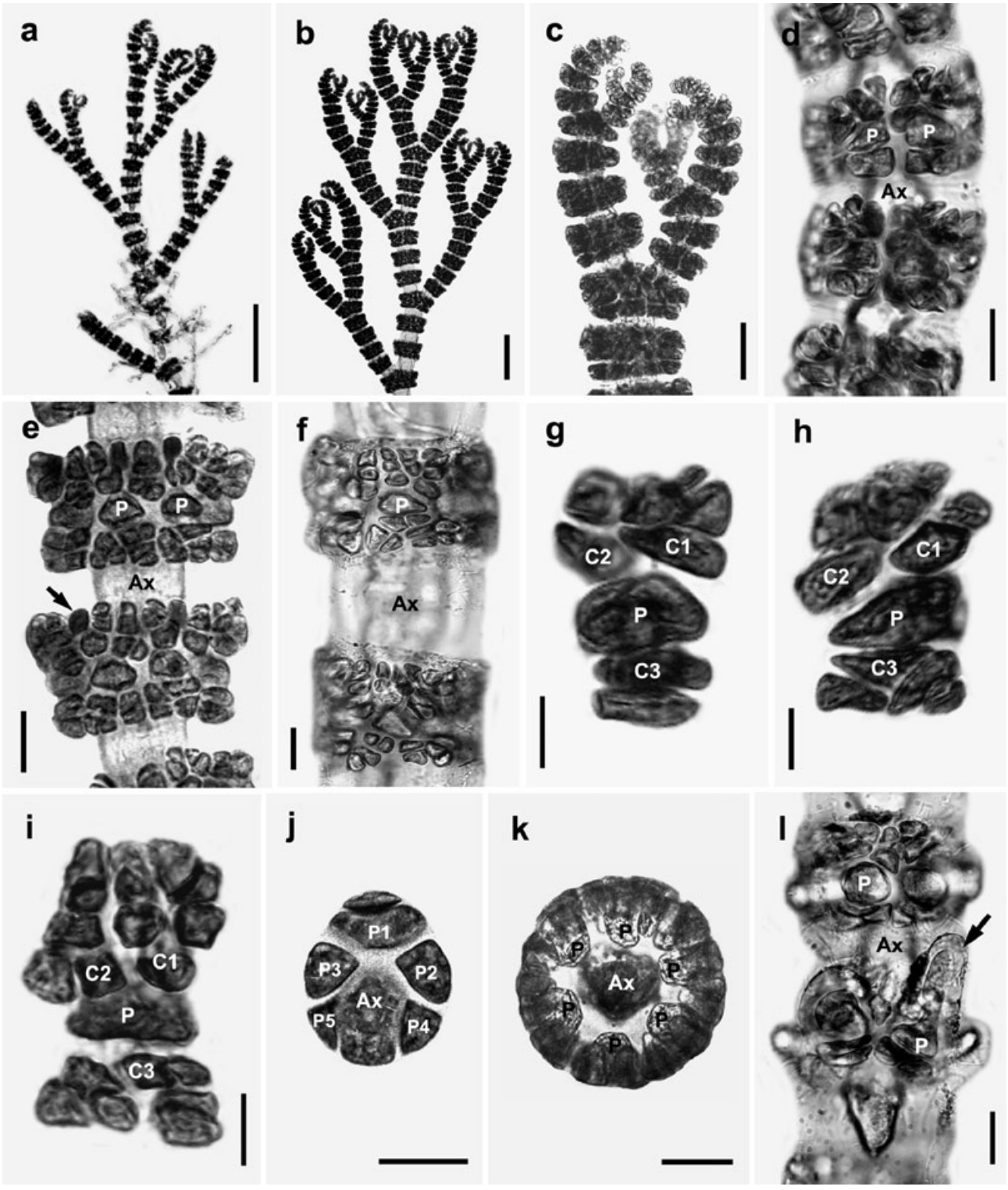

FIG. 4. *Gayliella taylorii* (Dawson) T. O. Cho et S. M. Boo, comb. nov. from California. (a) Thallus. Scale bar, 0.5 mm. (b) Upper thallus showing alternate branching pattern. Scale bar, 200 μm. (c) Apical region. Scale bar, 50 μm. (d–f) Incomplete cortication in upper (d), middle (e) with ovoid gland cells (arrow), and lower (f) parts. Scale bars, 20 μm. (g) Development of cortical initials showing alternate sequence formation and horizontal division of basipetal cortical initial. Scale bar, 10 μm. (h–i) Mature corticated produced from a periaxial cell. Scale bar, 10 μm. (j) Cross-sectional view of young thallus showing alternate sequence of periaxial cells produced from axial cell. Scale bar, 15 μm. (k) Cross-sectional view through cortical node of mature thallus. Scale bar, 25 μm. (l) Unicellular rhizoid (arrow) produced from periaxial cell. Scale bar, 20 μm. Ax, axial cell; C1–3, cortical initials, numbered by sequence of formation; P, periaxial cell; P1–5, sequence formation of periaxial cells.

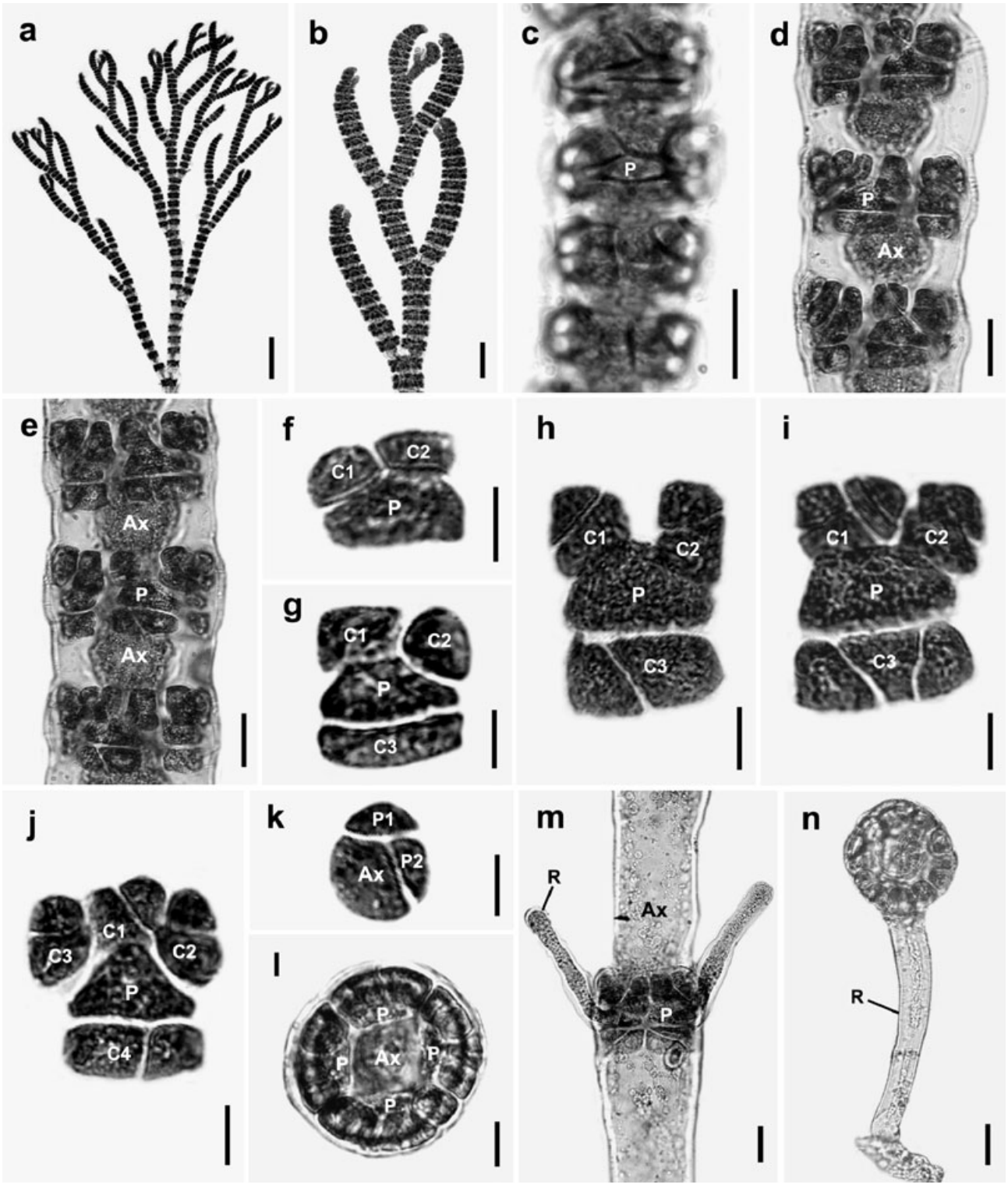

FIG. 5. *Gayliella transversalis* (Collins et Hervey) T. O. Cho et Fredericq, comb. nov. from Key West, Florida. (a) Thallus. Scale bar, 0.25 mm. (b) Apical region, Scale bar, 20 μm. (c–e) Incomplete cortication in upper (c), middle (d), and lower (e) parts. Scale bars, 20 μm. (f, g) Development of cortical initials showing alternate sequence of formation and horizontal division of basipetal cortical initial. Scale bar, 10 μm. (h, i) Mature cortications produced from a periaxial cell. Scale bars, 10 μm. (j) Mature cortication on branching point showing four cortical initials. Scale bar, 10 μm. (k) The early stage of formation of periaxial cells. Scale bar, 10 μm. (l) Cross-sectional view through cortical node of mature thallus. Scale bar, 10 μm. (m, n) Unicellular rhizoids with digitate tips produced from periaxial cell. Scale bars, 20 μm. Ax, axial cell; C1–4, cortical initials; P, periaxial cell; P1–2, sequence formation of periaxial cells; R, rhizoid.

and it is not a later homonym of *F. byssoides* Goodenough et Woodward (1797) (Silva et al. 1996).

Representative specimens examined: Key West, Florida, USA (LAF-30.x.03.1.1, T. O. Cho, 30.x.2003, vegetative and tetrasporic).

Thalli epiphytic, partly prostrate and partly erect, alternately branched, corticated only at the nodes; branching interval 5–6 for main axes, 8–10 for lateral axes; apices forcipulate, complanate; periaxial cells four; corticating filaments 3 per periaxial cell; basipetal cortical initial single, produced by horizontal division, 1 cell long (i.e., remaining undivided) rhizoids elongated, unicellular, terminating in digitate tip, produced from periaxial cells; tetrasporangia tetrahedral, produced from periaxial cells, adaxially arranged as a row, fully covered by acropetal cortical filaments.

Habit and anatomy: Thalli are 0.7–1.5 cm high, consisting of prostrate axes giving rise to erect axes (Fig. 5a). Erect axes bear forcipulate, incurved, and complanate apical regions (Fig. 5b). Axial cells are spherical to cylindrical, reaching 53 ± 8 μm × 61 ± 3 μm at the level of the seventh dichotomy away from the apex. Four periaxial cells are cut off obliquely from the upper part of each parent axial cell (Fig. 5, k and l) and remain at the nodes after axial cell elongation. The cortex is incomplete and banded (Fig. 5, c–e), the bands reaching 41 ± 2 μm × 64 ± 5 μm (L × W) at the level of the seventh branching point away from the apex. Three cortical initials are produced per periaxial cell in an alternate sequence (Fig. 5g) and develop into corticating filaments (Fig. 5i). The first two cortical initials are cut off obliquely from the anterior end of the periaxial cells and grow acropetally (Fig. 5, f–i); the remaining one is produced horizontally from the posterior end (Fig. 5, g–i). At the branching point, four cortical initials are produced from a single periaxial cell in alternate sequence: three acropetal initials and one basipetal initial (Fig. 5j). The acropetal corticating filaments are 2 cells long, while the basipetal one is short, 1 cell long.

Branches are alternately arranged and determinate (Fig. 5, a and b). Branching takes place at intervals of 5–6 (average 5.9 ± 0.3) axial cells in the main axes and at intervals of 8–10 (average 8.2 ± 0.4) cells in the lateral axes. Rhizoids attached to other algae are unicellular and elongate with a terminal digitate pad and are produced from periaxial cells of interwoven prostrate axes in the lower part of main axes (Fig. 5, m and n).

Tetrasporangia are adaxially arranged as a row on upper thallus parts and the axes with tetrasporangia are curved abaxially (Fig. 6, a–c); very rarely tetrasporangia are whorled at some nodes (Fig. 6d). One tetrasporangium is produced per periaxial cell (Fig. 6e) and covered by acropetal cortical filaments. Tetrasporangia are tetrahedrally divided, spherical to ellipsoidal, and average 34 ± 4 μm × 32 ± 4 μm excluding the sheath and 43 ± 5 μm × 40 ± 4 μm with the sheath.

Male and female thalli were not seen in our collections.

Gayliella womersleyi T. O. Cho, Maggs et L. McIvor, sp. nov. (Figs. 7, a–o; 8, a–d).

Thalli epiphytici, partim prostrati et partim erecti; alternatim ramose corticati solum ad nodos; intervallum ramificans 4–5 ad lateralem axes 7–9; apices forcipulati, apices forcipulatae, tortae; periaxiales cellulae 6–7; glandes cellulae ovoidae; fila corticata 3-numerata per periaxiales cellulas; basipetalinum initium 1-numerata, formata per divisionem

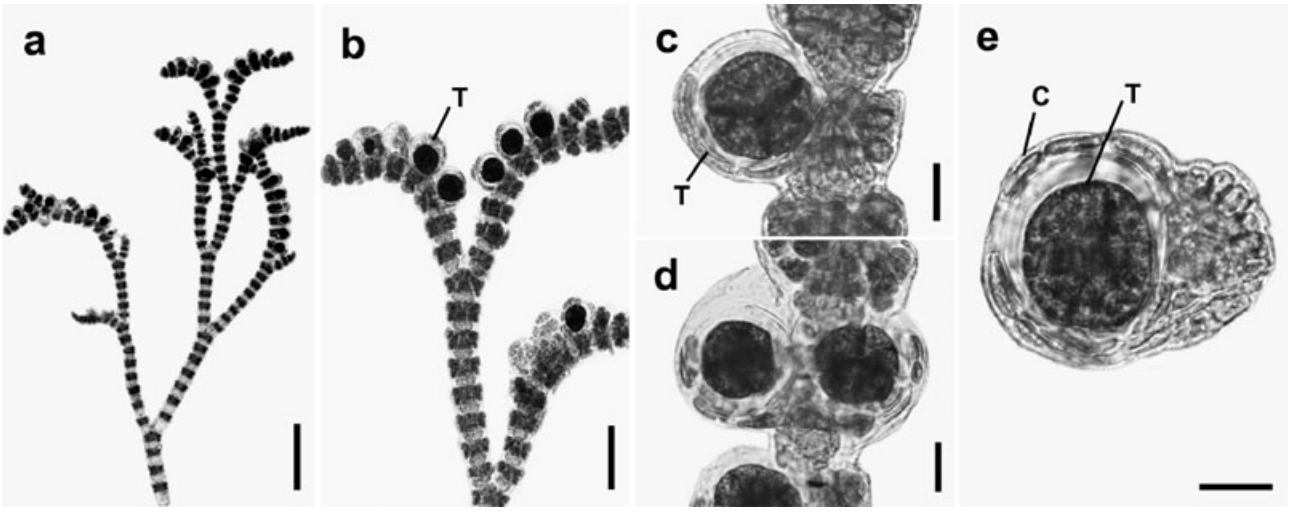

FIG. 6. *Gayliella transversalis* (Collins et Hervey) T. O. Cho et Fredericq, comb. nov. from Key West, Florida. (a) Tetrasporic plant. Scale bar, 0.25 mm. (b) Upper part of tetrasporic plant showing adaxial arrangement of tetrasporangia. Scale bar, 100 μm. (c) Tetrasporangium on the adaxial side. Scale bar, 20 μm. (d) Two tetrasporangia on the node. Scale bar, 20 μm. (e) Cross-sectional view of the node showing tetrasporangia produced from periaxial cells. Scale bar, 20 μm. C, cortical cell; T, tetrasporangium.

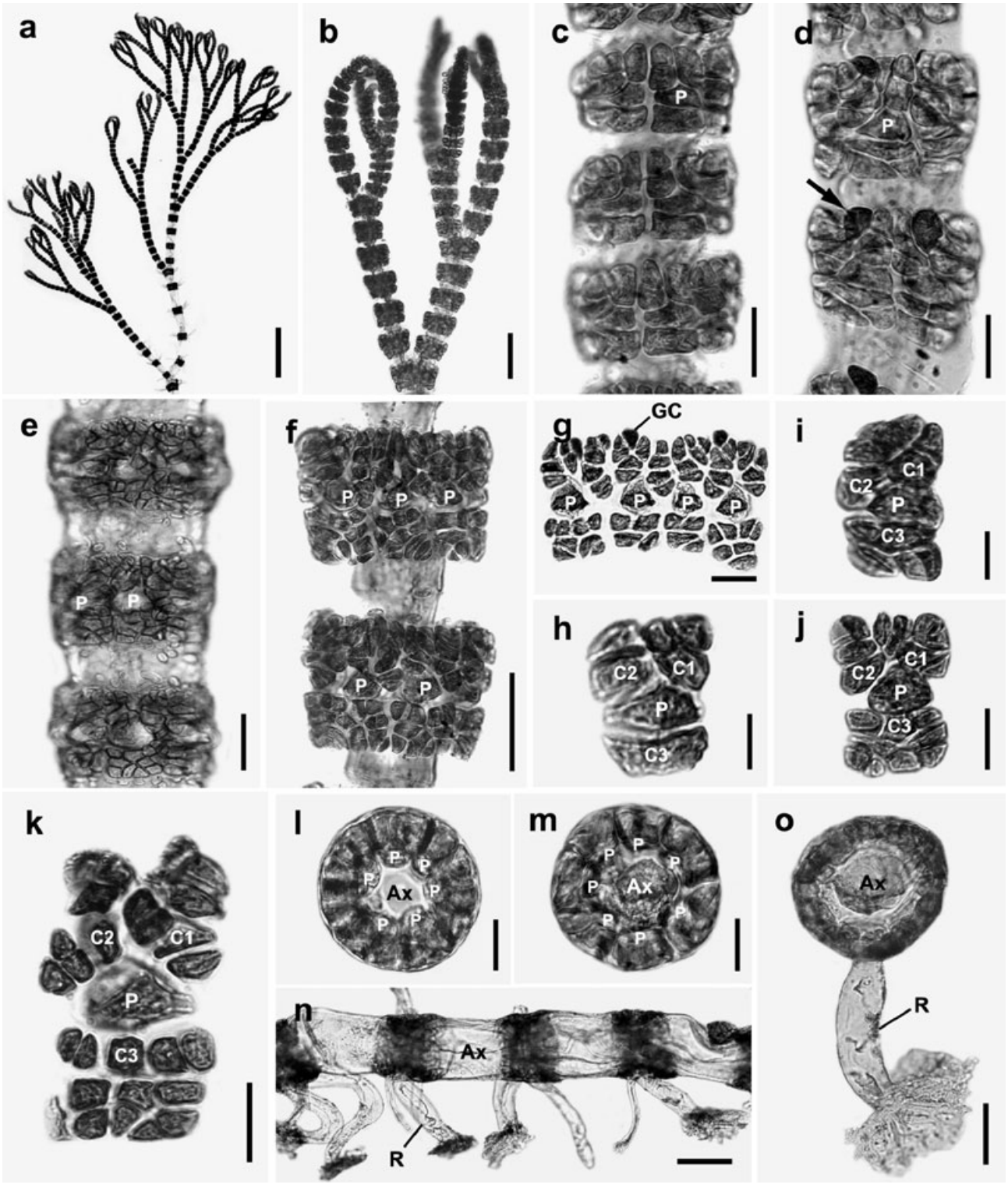

FIG. 7. *Gayliella womersleyi* T.O. Cho, Maggs et L. McIvor, sp. nov. from Australia. (a) Thallus. Scale bar, 0.5 mm. (b) Upper thallus showing the twisted branches. Scale bar, 100 μm. (c, d) Incomplete cortication with ovoid gland cells (arrow) in upper part. Scale bars, 20 μm. (e, f) Incomplete cortication in middle (e) and lower (f) parts. Scale bars, 50 μm. (g) Cortical node. Scale bar, 20 μm. (h, i) Development of cortical initials showing alternate sequence formation and horizontal division of basipetal cortical initials. Scale bars, 10 μm. (j, k) Mature corticationes produced from a periaxial cell. Scale bar, 20 μm. (l, m) Cross-sectional views through cortical node of mature thallus. Scale bars, 20 μm. (n) Creeping thallus with rhizoids with digitate tips on the node. Scale bar, 100 μm. (o) Cross-sectional view showing unicellular rhizoid produced from periaxial cell. Scale bar, 50 μm. Ax, axial cell; C1–3, cortical initials, numbered by sequence of formation; GC, gland cell; P, periaxial cell; R, rhizoid.

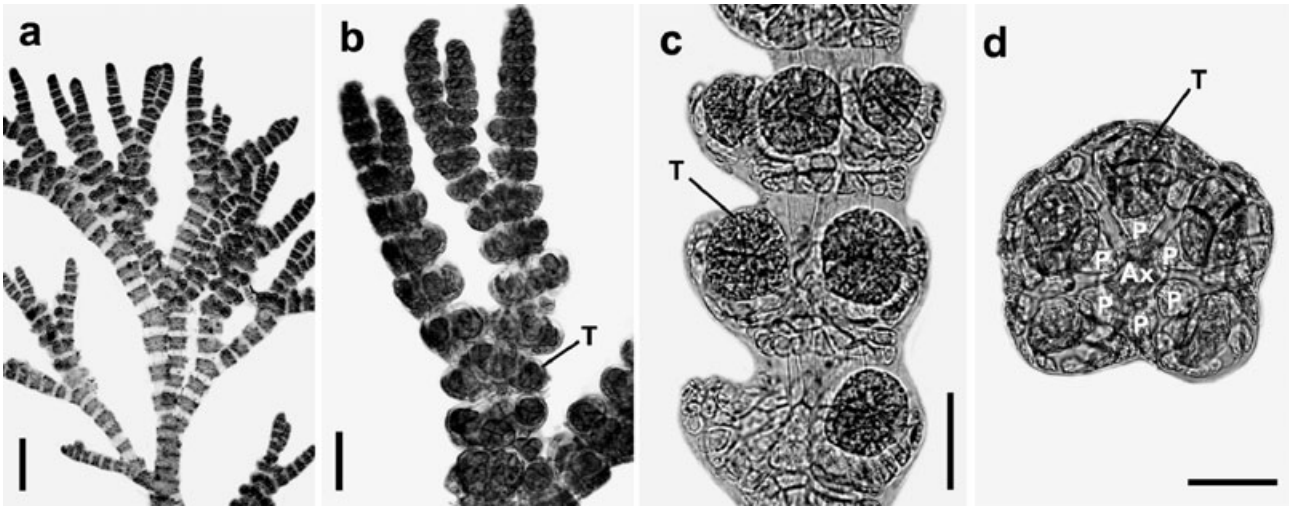

FIG. 8. *Gayliella womersleyi* T. O. Cho, Maggs et L. McIvor, sp. nov. from Australia. (a) Tetrasporic plant. Scale bar, 0.25 mm. (b) Upper part of tetrasporic plant showing adaxial arrangement of tetrasporangia. Scale bar, 100 μm. (c) Tetrasporangia in whorled arrangement on the node. Scale bar, 50 μm. (d) Cross-sectional view showing single tetrasporangium produced from each periaxial cell. Scale bar, 40 μm. Ax, axial cell; P, periaxial cell; T, tetrasporangium.

horizontalem, 3–4 cellulosum longum; rhizoidea elongata, unicellularia, apice digitato, formata cellulis periaxialus; tetrasporangia tetraedrica, formata cellulis periaxialibus, tecta omnino per fila corticalia acropeta.

Thalli epiphytic, partly prostrate and partly erect, alternately branched, corticated only at the nodes; branching interval 4–5 in main axes, 7–9 in lateral axes; apices forcipulate, twisted; periaxial cells 6–7; gland cells ovoid; corticating filaments 3 per periaxial cell; basipetal cortical initial single, produced by horizontal division, 3–4 cells long; rhizoids elongated, unicellular, terminating in digitate tip, produced from periaxial cells; tetrasporangia tetrahedral, whorled at the node, produced from periaxial cells, fully covered by acropetal cortical filaments.

Type locality: Williamstown, S. Australia.

Type: coll. by M. D. Guiry, 13.iii.2002, #1507, vegetative; holotype on slide at LAF (LAF-13.iii.02-1-1).

Etymology: Named in honor of Dr. H. B. S. Womersley, prominent phycologist and specialist in the taxonomy and floristics of Australian seaweeds.

Representaive specimens examined: Williamstown, S. Australia (M. D. Guiry, 13.iii.2002, #1507, vegetative); Tamarama, NSW Australia (G. Zuccarello, 20.viii.2001, vegetative and tetrasporic).

Habit and anatomy: Thalli are 0.5–0.8 cm high, consisting of prostrate axes giving rise to erect axes (Fig. 7a). Erect axes bear forcipulate, incurved, and twisted apical regions (Fig. 7b). Axial cells are spherical to cylindrical, reaching 91 ± 10 μm × 66 ± 6 μm (L × W) at the level of the seventh branch point away from the apex. Six or seven periaxial cells are cut off obliquely from the upper part of each parent axial cell (Fig. 7, l and m) and remain at the nodes after axial cell elongation. The cortex is incomplete and banded (Fig. 7, c–g), bands reaching 80 ± 4 μm × 129 ± 5 μm (L × W) at the seventh branching point away from the apex. Three cortical initials are produced from each periaxial cell in an alternate sequence (Fig. 7h) and develop into corticating filaments (Fig. 7, i–k). The first two cortical initials are cut off obliquely from the anterior end of the periaxial cells and grow acropetally and basipetally; the remaining one is produced horizontally from the posterior end of the periaxial cell and grows basipetally and horizontally (Fig. 7, h–k). The acropetal corticating filaments are 4–5 cells long, while the basipetal ones are 3–4 cells long.

Branches are regularly alternate and indeterminate (Fig. 7a). Branching takes place at intervals of 4–5 (average 4.6 ± 0.5) axial cells in the main axes and at intervals of 7–9 (average 8.0 ± 0.4) cells in the lateral axes. Gland cells develop from cortical cells of acropetally corticating filaments and are spherical to ovoid (Fig. 7, d and g), averaging 20 ± 2 μm × 12 ± 2 μm. Rhizoids are unicellular with a terminal digitate pad (Fig. 7n), and each rhizoid is produced from a periaxial cell (Fig. 7o) of prostrate axes and the lower parts of the main axes.

Tetrasporangia are distributed on upper thallus parts (Fig. 8a) and whorled at the nodes (Fig. 8b). A single tetrasporangium normally develops per periaxial cell (Fig. 8, c and d), and it is covered by an acropetal cortical filament. Tetrasporangia are tetrahedrally divided, spherical to ellipsoidal (Fig. 8d), and average 44 ± 2 μm × 41 ± 3 μm.

Male and female thalli were not found in our collections.

Key to these select species of *Gayliella*

1a. Periaxial cells 4, basipetal cortical filament 1 cell long, cortex <70 μm long	2
1b. Periaxial cells 5–7, basipetal cortical filament 2–4 cells long, cortex >90 μm long	3
2a. Branching intervals 4–5 on main axes, 4–6 on lateral axes	*G. mazoyerae*
2b. Branching intervals 5–6 on main axes, 8–10 on lateral axes	*G. transversalis*
3a. Gland cells clavate, cortex >140 μm width diam.	*G. fimbriata*
3b. Gland cells spherical to ovoid, cortex <130 μm width diam.	4
4a. Apices twisted	*G. womersleyi*
4b. Apices complanate	5
5a. Branching intervals 7–9 on main axes, 10–14 on lateral axes	*G. flaccida*
5b. Branching intervals 3–4 on main axes, 4–6 on lateral axes	*G. taylorii*

Phylogenetic analysis based on rbcL and partial LSU rDNA. The 1,442 bp portion of the *rbc*L gene analyzed included 388 parsimony-informative sites without the outgroups. Phylogenetic analyses based on *rbc*L showed that sequences attributed to *Gayliella* gen. nov. formed a supported monophyletic clade, separate from *Ceramium* and the other Ceramieae taxa. MP analyses of the *rbc*L alignment (Fig. 9) were congruent with the Bayesian tree (not shown). *G. mazoyerae* from Sicily is the sister taxon of *G. transversalis* from the Florida Keys, and both in turn are sister to the unnamed species from Brazil tentatively assigned the name ''*C. flaccidum.*'' Two species given the name ''*C. dawsonii*'' are more closely related to the *G. flaccida* from Ireland, whereas ''*C. dawsonii*''-1 clusters with the Pacific group consisting of *G. taylorii* from California and *G. womersleyi* from S. Australia, but this relationship is weakly supported. *G. fimbriata* from Baja California, Mexico, is always positioned as a sister group to the rest of the *Gayliella* clade. A partial 847 bp fragment of the LSU rDNA data set was also analyzed that included 177 parsimony-informative sites excluding the Antithamnieae outgroup. The ML tree inferred from partial LSU rDNA sequences (Fig. 10) grouped members of the new genus *Gayliella* with high bootstrap support, again distinct from other *Ceramium* species.

DISCUSSION

Recent morphological studies (Cho et al. 2002, Barros-Barreto et al. 2006) suggested that the *C. flaccidum* complex might be recognized as an assemblage distinguished from other *Ceramium* species. Although *C. flaccidum* was originally described as *Hormoceras flaccidum* Kützing 1862, the generic name *Hormoceras* Kützing (1842) applies to a different group of *Ceramium* species. Nakamura (1950, p. 155) designated *Ceramium diaphanum* (Lightfoot) Roth (*Conferva diaphana* Lightfoot) as the lectotype of *Ceramium* subg. *Hormoceras* (Kützing) Nakamura. This species is allied with *Ceramium virgatum* Roth, the generitype of *Ceramium*. Because no generic name is available to accommodate the *C. flaccidum* complex, we propose *Gayliella* as a new genus.

The new genus *Gayliella* gen. nov. is characterized by production of three cortical initials per periaxial cell, of which the basipetal initial divides horizontally (Fig. 11, a and b); unicellular and elongate rhizoids produced from periaxial cells and terminating in a pad-like structure (Fig. 11d); alternate branching; incomplete cortication (Fig. 11c); spermatangial parent cells formed from cortical cells (Fig. 11e), carposporophyte surrounded by involucral branchlets (Fig. 11f), and tetrasporangia formed by periaxial cells and fully covered with cortical cells (Fig. 11g).

Gayliella has three cortical initials per periaxial cell, and, of these, the basipetal cortical initial is produced by horizontal division. Among members of the tribe Ceramieae, *Centroceras* shares the character of three cortical filaments per periaxial cell (Hommersand 1963, Norris 1993). However, *Centroceras* is distinguished from *Gayliella* by having complete cortication and basipetal cortical cells produced by oblique divisions (Hommersand 1963). *C. procumbens* has three cortical initials as in *Gayliella* (Cho et al. 2001b), but its basipetal cortical initial differs in that it divides longitudinally. In most species of the Ceramieae, except *Centroceras* and some *Ceramium* species, 4–5 cortical initials are cut off from each periaxial cell, and the basipetal cortical initials are produced by oblique division (Hommersand 1963, Womersley 1978, Abbott 1999, Cho et al. 2001a, 2004).

All members of the genus *Gayliella* have unicellular and elongate rhizoids produced only from periaxial cells with each rhizoid terminating in a digitate tip, while in *Ceramium* species both periaxial and cortical cells form multicelullar rhizoids terminating in digitate or discoid pads (Nakamura 1965, Womersley 1978, Cho et al. 2001a,b). Although a few species within the Ceramieae, such as *Reinboldiella schmitziana* (Reinbold) De Toni (1895) and *Carpoblepharis flaccida* (J. V. Lamouroux) Kützing (1849), also have unicellular rhizoids (Hommersand 1963), their rhizoids differ from those of *Gayliella*, being formed from superficial cortical cells and lacking digitate tips.

Most of the genera in the tribe Ceramieae are reported to have similar female and male reproductive organs (Boo and Lee 1994), except that spermatangia are produced from monosiphonous filaments borne on periaxial cells in *Centroceras*. Most reproductive stages in *Gayliella* (Fig. 11, e–g) are similar to those in *Ceramium* (Nakamura 1965, Abbott 1999, Cho et al. 2002); however, the development of tetrasporangia in *Gayliella* may differ from that of *Ceramium*. One tetrasporangium originates per peri-

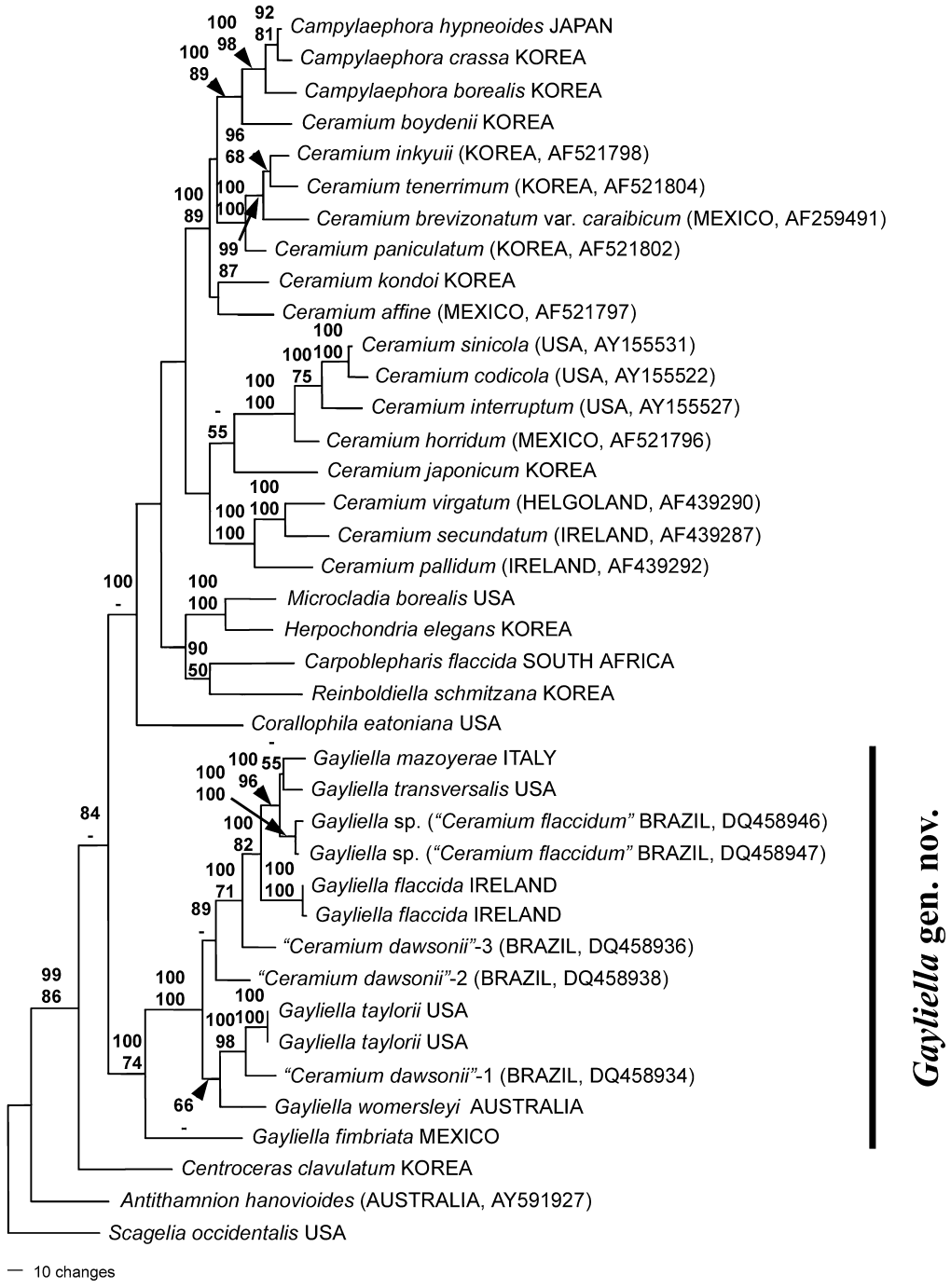

FIG. 9. One of two most-parsimonious trees inferred from *rbc*L sequence analysis showing the phylogenetic position of the genus *Gayliella* within the tribe Ceramieae. Tree length = 1,818; consistency index = 0.36; retention index = 0.58. Bootstrap proportion values (>50%) are shown at bottom of internal branches, and Bayesian a posteriori probabilities on top.

axial cell and is covered by cortical filaments in *Gayliella* (Fig. 11g). In typical *Ceramium* species with complete or interrupted cortication, tetrasporangia develop from inner cortical cells as well as from each periaxial cell, whereas in most incompletely corticated *Ceramium* species, 2–3 tetrasporangia develop only from periaxial cells (Cho et al. 2001a, 2003a). Accordingly, the single, fully covered tetrasporangium formed only by periaxial cells is a further feature distinguishing the *Gayliella* species from most *Ceramium* species.

Even though Womersley (1978) recognized current *Gayliella* species as encompassing the single species *C. flaccidum*, there are sufficient features to

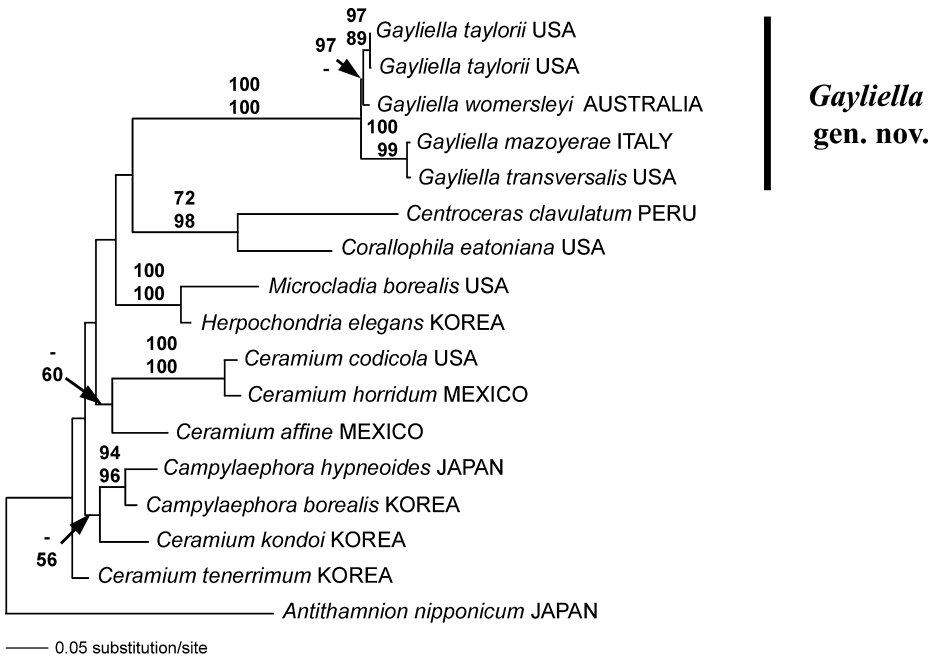

FIG. 10. Phylogenetic position of the genus *Gayliella* within Ceramieae inferred from maximum-likelihood (ML) analyses of LSU rDNA sequences. Bootstrap proportion values (>50%) for maximum–parsimony (top) and ML (bottom) are shown at the nodes.

justify recognition of these taxa as separate species based on their detailed morphology (Table 1). *G. flaccida* is similar to *G. taylorii* and *G. womersleyi* in the shape of the cortex; however, the lateral branches of *G. flaccida* have the largest number of axial cells between branching points (10–14) and show indeterminate growth. In particular, lateral determinate branches are alternately arranged, and they are longer than main axes. *G. fimbriata* is similar to *G. taylorii* and *G. womersleyi* in its branching pattern but is distinct in having clavate gland cells. Gland cells of *G. fimbriata* are also generally longer and broader than those of other *Gayliella* species and erupt from the cortex. Our *Gayliella* collections from Key West agree with the description of *C. transversale* described by Collins and Hervey (1917, p. 145–47, pl. V, figs. 29–31 of plate V) from Bermuda. *G. transversalis* is distinct in its short basipetal cortication, which is one cell long, and has alternately arranged lateral determinate branches.

Tetrasporangial plants of *G. transversalis* are also identifiable, since tetrasporangia of the other *Gayliella* species are whorled, but those of *G. transversalis* are arranged adaxially. Only a few specimens of *G. mazoyerae* were suitable for vegetative morphological study. Although these did not provide enough information to assess the development of cortication in detail, *G. mazoyerae* is similar to *G. transversalis* in its short basipetal cortication and the number of periaxial cells. *G. mazoyerae* is distinguished from *G. transversalis* in having lateral branches with regular branching and in the small number (4–6) of axial cells between branching points.

Our *G. taylorii* collections agree with the description of Mexican material by Dawson (1950). The cortication pattern of *G. taylorii* is not easily separated from that of *G. womersleyi* and *G. flaccida* because of their similar-sized cortex, but the branching pattern of *G. taylorii* differs from these two species in the small number of axial cells (3–4 in main axis; 4–6 in lateral axis) between branching points. *G. womersleyi* is distinguished from other *Gayliella* species by its twisted apical region. Therefore, *G. flaccida*, *G. fimbriata*, *G. transversalis*, *G. mazoyerae*, *G. taylorii*, and *G. womersleyi* are recognizable as separate species in the genus *Gayliella*. The species referred to as *C. flaccidum* from Brazil by Barros-Barreto et al. (2006) is clearly distinct from material from the type locality and from the other members of *Gayliella* described here. Likewise, the report of *C. dawsonii* Joly in Barros-Barreto et al. (2006) comprises more than one species as inferred from *rbc*L sequence analysis. Since we have not studied topotype material from Saõ Paulo State to ascertain which of the three samples is genuine *C. dawsonii*, we have opted to refer to the three Brazilian taxa that are clearly *Gayliella* species as *"C. dawsonii."*

Cho et al. (2002) showed that *C. recticorticum* Dawson is very similar to *G. flaccida* (as *C. flaccidum*), *G. fimbriata* (as *C. fimbriatum*), and *G. mazoyerae* (as *C. gracillimum* var. *byssoideum*) in its basipetal cortical initials and rhizoids. Although it is not included in this study, *C. recticorticum* is here transferred to the

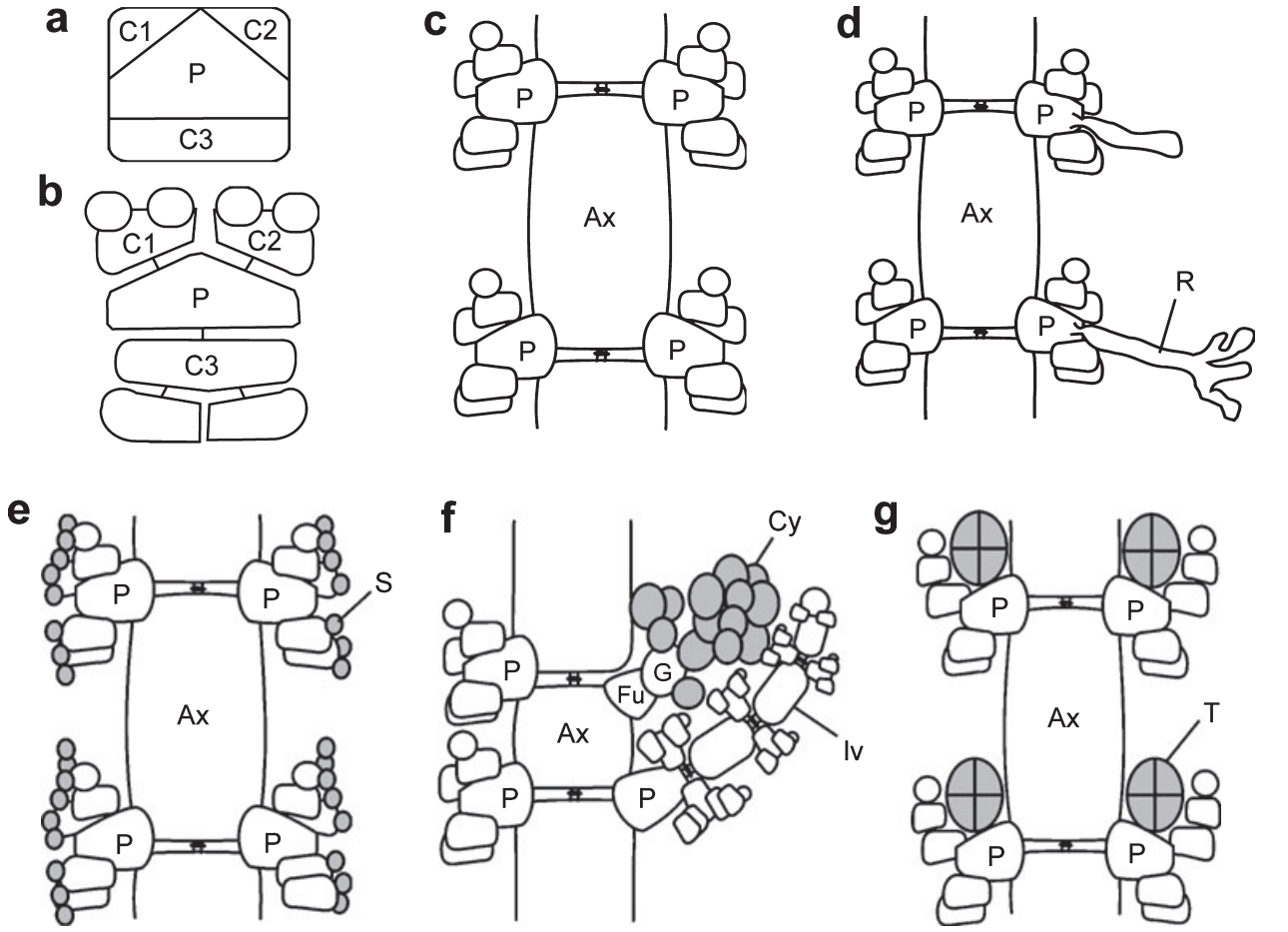

FIG. 11. Diagnostic characters of *Gayliella* gen. nov. (a) Formation of cortical initials. (b) Cortical filament formation from single periaxial cell. (c) Cortical node showing incomplete cortex. (d) Rhizoid position showing formation from periaxial cells. (e) Spermatangial position showing formation from cortical cells. (f) Carposporophyte position with involucral branchlet. (g) Tetrasporangial position showing formation from periaxial cells. Ax, axial cell; C1–3, cortical initials, numbered by sequence of formation; Cy, cystocarp; Fu, fusion cell; G, gonimoblast; Iv, involucral branchlet; P, periaxial cell; R, rhizoid; S, spermatangium; T, tetrasporangium.

genus *Gayliella* based on previous morphological observations by Cho et al. (2002).

Gayliella recticortica (Dawson) T. O. Cho et S. M. Boo comb. nov.

Basionym: *C. recticorticum* Dawson 1950, p. 124, pl. 3, figs. 23–24.

Type locality: Bahia Bocochibampo, near Guaymas, Sonora.

Holotype: Dawson. no. 1769, LAM 500108 (AHFH 48795).

Our phylogenetic analyses of *rbc*L (Fig. 9) and LSU rDNA (Fig. 10) gene sequence analyses show that *Gayliella* represents a monophyletic clade composed of about 10 species, including four tentative species from Brazil: *G. flaccida, G. fimbriata, G. transversalis, G. mazoyerae, G. taylorii, G. womersleyi, G.* sp. from Brazil, and ''*C. dawsonii*''-1, ''*C. dawsonii*''-2, and ''*C. dawsonii*''-3 from Brazil. The morphological similarity of the species was reflected in the phylogenetic analyses. Although some other taxa in the tribe Ceramieae were not supported by high bootstrap values, in all analyses, members of *Gayliella* formed a clade with high bootstrap support. The phylogenies indicate that the genus *Ceramium* is not monophyletic and is in need of a major systematic overhaul. The inclusion of additional *Gayliella* taxa worldwide in an expanded data set will be required to begin an assessment of the taxonomy and a reconstruction of any global biogeographic history of the genus in the future.

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TABLE 1. Comparison of morphological features among the genus *Gayliella* gen. nov. species.

	G. flaccida	*G. fimbriata*	*G. mazoyerae*	*G. taylorii*	*G. transversalis*	*G. womersleyi*
Thallus length (cm)	0.3–12	0.5–1.2	0.9	0.7–1.2	0.7–1.5	0.5–0.8
Apex	Complanate	Complanate	Complanate	Complanate	Complanate	Twisted
Axial cell						
Average size of axial cell (μm, L × W)	84 ± 5 × 57 ± 5	214 ± 43 × 89 ± 11	80 ± 12 × 65 ± 8	97 ± 11 × 55 ± 9	53 ± 8 × 61 ± 3	91 ± 10 × 66 ± 6
Average no. axial cells between branches along main axis	7.0 ± 0.9	3.5 ± 0.6	4.1 ± 0.3	3.8 ± 0.4	5.9 ± 0.3	4.6 ± 0.5
Average no. axial cells between branches along lateral axis	11.8 ± 1.5	5.2 ± 0.7	4.9 ± 0.5	5.3 ± 0.5	8.2 ± 0.4	8.0 ± 0.4
Cortical node						
Average size of cortical band (μm, L × W)	66 ± 5 × 99 ± 11	93 ± 10 × 169 ± 26	38 ± 3 × 56 ± 4	63 ± 2 × 101 ± 2	41 ± 2 × 64 ± 5	80 ± 4 × 129 ± 5
No. cortical cells growing acropetally	3–4	3–4	1–2	3–4	2	4–5
No. cortical cells growing basipetally	2–3	2–3	1	2–3	1	3–4
Periaxial cell number	5–6	6–7–8	4	6–7	4	6–7
Gland cell						
Shape	Ovoid	Clavate	Ovoid	Ovoid	–	Ovoid
Average size (μm, L × W)	12 ± 3 × 8 ± 2	59 ± 15 × 8 ± 2	9.8 ± 0.7 × 14 ± 0.9	11 ± 2 × 11 ± 1	–	20 ± 2 × 12 ± 2
Tetrasporangia						
Arrangement	Adaxial	Whorled	–	–	Adaxial	Whorled
Average size (μm, L × W)	40–80 (W)	35 (W)	–	–	43 ± 5 × 40 ± 4	44 ± 2 × 41 ± 3
References	This study, Maggs and Hommersand (1993)	This study, Abbott (1999)	This study	This study	This study	This study

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Supplementary Material

The following supplementary material is available for this article:

Table S1. Taxa and collection information of samples used in the analyses of *rbc*L and LSU rDNA with their GenBank accession numbers.

This material is available as part of the online article from: http://www.blackwell-synergy.com/doi/abs/10.1111/j.1529-8817.2008.00505.x.

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