Two creeping Ceramium species (Ceramiaceae, Rhodophyta) from the Florida Keys: C. reptans sp. nov. and recircumscription of C. codii (Richards) Mazoyer

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On the basis of comparative morphology, a new creeping Ceramium species with incomplete and narrow nodal cortication, C. reptans sp. nov., is described from the Florida Keys, USA, where it co-occurs epiphytically with C. codii on the same host, Hypnea spinella. Ceramium reptans sp. nov. is recognized by a prostrate axis producing unbranched upright axes dorsally; five perialgal cells per axial cell; three cortical cells cut off per perialgal cell, with the first acropetal cortical cell becoming the pseudoperiarchal cell that extends longitudinally parallel to the level of neighboring perialgal cells, a second acropetal and third basipetal horizontal cortical cell; and cruciately divided tetrasterogonia in whorls bulging from a single node pressed to the contiguous node below on upright axes, 3–6 segments below the apex. Ceramium codii, described from Bermuda, is recognized by a prostrate axis producing unbranched, upright axes dorsally, four perialgal cells per axial cell, three cortical cells cut off per perialgal cell with the basipetal cortical cell cut off horizontally on the prostrate axis, and 1–2 tetrahedrally divided tetrasterogonia produced per perialgal cell. Among the described creeping Ceramium species; C. codii, C. bisporum, C. cingulatum, C. cingulum, C. dorsiventrale, C. inescipicum, C. jolyi, C. luetzelburgii, C. procumbens, C. poepigianum, C. puniciforme, C. serpens, and C. tenerimum var. brevizonatum f. repens, none has the characteristic pseudoperiarchal cells of C. reptans. Ceramium codii may not be a widespread species as is widely reported in the literature.

Key Words: Bermuda, Ceramium, C. codii, C. reptans sp. nov., Ceramiales, Florida, Morphology, Rhodophyta, Seaweed, Taxonomy

INTRODUCTION

The species-rich genus Ceramium Roth is characterized vegetatively by axial cells incompletely to completely covered by cortical cells and by a thallus composed of pseudodichotomously branching or by prostrate axes bearing erect axes. Female gametophytes produce cystocarps surrounded by finger-like involucral branches, male thalli have spermatangia produced first on the adaxial side and later in whorls along the axis, and tetrasterophoruses bear tetrasterogonia cut off from perialgal cells or irregularly from cortical cells, and are naked or covered by cortical cells (see Maggs & Hommersand 1993 for a detailed description of the genus).

In the tropical and subtropical western Atlantic, including the Gulf of Mexico, about 28 species of Ceramium are currently recognized (Wynne 2005). Ballantine (1990, p. 146) recently described a new repent species from Puerto Rico in the Caribbean Sea, C. bisporum, which has also been reported from the Mediterranean (Sartoni & Boddi 2002). Worldwide, there are additional diminutive, creeping epiphytic species characterized by a predominantly prostrate habit bearing determinate upright axes, including C. codii (Richards) Mazoyer (1938, p. 324) described from Bermuda; C. dorsiventrale Hommersand (1963, p. 234) originally described from Trinidad; C. jolyi (Diaz-Piferer) Ballantine & Wynne (1986, p. 500) described from Puerto Rico; C. cingulatum Weber-van Bosse (1923, p. 332) described from Indonesia; C. cingulum Meneses (1995, p. 170) described from the Hawaiian islands; C. inescipicum Zanardini (1839, p. 136) from the Mediterranean Sea (Cormaci et al. 1994, p. 1001); C. luetzelburgii Schmidt (1924, p. 98) described from Brazil; C. poepigianum Grunow (1867, p. 64) described from South Africa; C. procumbens Setchell & Gardner (1924, p. 772) described from the Gulf of California, which was recently characterized and illustrated by Cho et al. (2001); C. puniciforme Setchell (1924, p. 158) from the Gulf of California; C. serpens Setchell & Gardner (1924, p. 775) from the Gulf of California; and Ceramium sp. reported from the Mediterranean (Coppejans 1977; as C. tenerimum (Mertens) Okamura var. brevizonatum (H.E. Petersen) G. Feldmann f. repens, Coppejans 1983, pl. 146A–B).

Ceramothamnion codii was poorly described from Bermuda as growing on Codium tomentosum Stackhouse by Richards (1901, p. 264) and then transferred to Ceramium by Mazoyer (1938, p. 324). Subsequently, this species has been recognized as being widely distributed in warm temperate and tropical areas (Boo & Lee 1994) such as Hawaii (Abbott 1999), southern Japan (Isono 1972), eastern Australia (Cribb 1983; Millar 1990), Mediterranean Sea (Feldmann-Mazoyer 1940), Aegean Sea (Athanasiadis 1987), Atlantic Spain (Gallardo et al. 1985), Caribbean (Taylor 1960; Diaz-Piferer 1969), West Africa (Lawson & John 1982), and throughout the Indian Ocean (see Silva et al. 1996). The taxonomy of Ceramium codii is still in a state of chaos (see Sartoni & Boddi, 2002).
Two creeping Ceramium species comprising predominantly prostrate axes bearing unilaterial, unbranched upright axes were recently collected from the Florida Keys. In this paper, we describe one of the species as new to science, C. reptans sp. nov., and recircumscribe C. codii.

MATERIAL AND METHODS

We recently collected creeping specimens of two Ceramium species co-occuring epiphytically on several individuals of the same host, Hyphrea spinella (C. Agardh) Kützing, found in the drift in the Missouri Key–Ohio Key Channel, Florida Keys, Florida. All specimens were preserved in 4% formalin/seawater. Topotype material of C. codii, excicaca #1899, Phyctotheca Borealis-Americana, Collins, Holden & Setchell (1912) was examined and sectioned for comparative purposes.

Microscope observations were made from material stained with 1% aqueous aniline blue acidified with 0.1% diluted HCl. Vouchers were deposited in LAF (herbarium abbreviations follow Holmgren et al. 1990). Photomicrographs were taken with a Polaroid DMC Le digital camera (Polaroid, Inc., Cambridge, MA) attached to an Olympus BX60 (Olympus, Melville, NY). A total of 15 individuals were selected for quantitative measurements.

RESULTS

Ceramium reptans T.O. Cho & S. Fredericq, sp. nov. Figs 1–23

Thalli minute, epiphytic in Hyphrea spinella, constantes ex parte prostrata axe horizontali dorsali ramos adventitiis unilaterales erectis ventrali rhizoida producenti; axes erecti uniseriati extensi 0.8–1.2 mm; apices recti; rhizoida brevia disco 3–4 cellulare diametro; cortication incompleta, constantes ex 3 vel 4 seriis cellularum; cellulae peritaxiales 5; spermatangia ad apices ramorum erectorum cellulis parentalia spermatangiorum in cellulis corticalibus extinvis exorienteibus; tetrasporangia crassiora ad nodum unicum ramorum erectorum exoriente, singulatim in quoque cellula peritaxialis formata, protuderentia e nodo corticali 3–6 segmentis intra apicem, 38–42 μm diam., in vorticellis. Thalli minute, epiphytic on Hyphrea spinella, consisting of a prostrate portion with a horizontal axis adventitiously producing unilaterial upright branches dorsally and rhizoids ventrally, upright branches uniseriate, ranging from 0.8–1.2 mm; apices straight; rhizoids short with a 3–4 celled digestive pad; cortication incomplete, consisting of 3–4 cell rows; peritaxial cells 5 in number, each cutting off 2 ovoid acropetal and 1 flattened basipetal cortical cell, with the first cortical cell becoming the pseudoperiangular cell that continues to divide, growing parallel to and extending to the level of neighboring peritaxial cells; spermatangial clusters near apices of upright branches; spermatangial parent cells borne on the outermost cortical cells; tetrasporangial structures to a single node of the upright branches, with a single tetrasporangial initial cut off per peritaxial cell, protruding from a cortical node 3–6 segments below apex, cruciately divided, 38–42 μm in diameter, in whorls.


Etymology: The species is named for the creeping habit and characteristic pseudoperiangular cells.

Habit and Anatomy: Thalli are delicate and 0.8–1.2 mm high, consisting of prostrate axes bearing short erect axes. Apices are straight and unbranched, rarely pseudodichotomous (Figs 1–3) in the prostrate axes. Erect axes, comprising up to 15 segments, are unilaterally cut off from peritaxial cells on the dorsal side of the prostrate axis (Fig. 2). Axial cells are spherical to cylindrical, reaching 74 ± 5 μm × 31 ± 2 μm (L × W) at the level of the seventh cell away from the apex.

Five peritaxial cells are cut off obliquely from the upper part of each parent axial cell (Fig. 6) and remain at the nodes after axial cell elongation (Figs 4, 5). Each peritaxial cell produces three cortical cells by slightly oblique division, two acropetal cells and one basipetal cell (Fig. 7), in an alternate sequence (Figs 10, 11). The first cortical cell extends longitudinally parallel to the peritaxial cells, which it resembles, and becomes a pseudoperiangular cell (Figs 8, 9) that continues to divide. Whereas a single pseudoperiangular cell is located on one side of each peritaxial cell (Fig. 4), the first-formed peritaxial cell bears two pseudoperiangular cells bilaterally (Figs 6, 12). The third cortical cell is cut off horizontally from the lower end of each peritaxial cell (Figs 10, 11). Acropetal cortication is 1–2 cells long and basipetal cortication is absent or one-celled (Figs 4, 5). The cortex is incomplete and narrowly banded (Figs 4, 5), reaching 23 ± 3 μm × 43 ± 5 μm (L × W) at the level of the seventh cell away from the apex.

Rhizoids attached to the host are short and rod-shaped, cutting off 3–4 cells basally resulting in a digitate pad, produced from peritaxial cells at nearly every node on the ventral side of the prostrate axes (Figs 2, 13).

Reproductive Structures: In male plants, spermatangial parent cells develop from cortical cells in the upper part of the thallus and produce 1–2 spermatangia terminally (Figs 14, 15). Spermangia are organized in whorls surrounding several nodes of the erect axes (Fig. 15). Spermangia are colourless and elliptical to spherical, measuring 2 ± 1 × 2 ± 1 μm in size.

In tetrasporic plants, tetrasporangia are restricted to a single node, 3–6 segments below the apex of the erect axis (Figs 16, 17). A single tetrasporangium is cut off per peritaxial cell (Figs 18, 19). Tetrasporangia are produced in an alternate sequence resulting in a whorl around the axis (Figs 20–22). The cortical node bearing the tetrasporangia is tightly appressed to the node below (Figs 18, 19). The acropetal cortical filaments bearing tetrasporangia are elongated and 3–4 cells long each (Fig. 23), and the tetrasporangia are almost completely covered by them (Fig. 20). Tetrasporangia are cruciately divided, spherical to ellipsoidal, and average 41 ± 1 μm × 40 ± 2 μm excluding the sheath and 45 ± 2 μm × 44 ± 2 μm with the sheath.

Female gametophytes and carposporophytes are unknown.

Ceramium codii (Richards) Mazoyer 1938: p. 324

Figs 24–55

Typotype: Figs. 47–55; excicata nr. 1899, as Ceramothamnion codii Richards, Phyctotheca Borealis-Americana, Collins, Holden & Setchell, on Codium tomentosum, Cooper’s Island, April 29, 1912. This material contains cystocarps, antheridia and tetraspores. Material, also from Bermuda, was distributed as P.B.-A. No. 845' (LAB).
Figs 1–13. Vegetative structures (LAF-31-10-2004-1-2; slides 1, 2, 7) of *Ceramium reptans* T.O. Cho & S. Fredericq. Ax, axial cell; C1–3, sequence of cortical cell formation; P, periaxial cell; Ps, pseudoperiaxial cell.

Figs 1–2. Prostrate axes bearing short unbranched, erect axes. Scale bars = 100 μm (Fig. 1) or 200 μm (Fig. 2).

Fig. 3. Apical region of prostrate axis showing pseudodichotomous branching pattern. Scale bar = 20 μm.

Figs 4–5. Incomplete cortication in middle (Fig. 4) and lower (Fig. 5) part of erect axes. Scale bars = 20 μm.

Fig. 6. Cross-section through cortical node of erect axis showing five periaxial and six pseudoperiaxial cells. Scale bar = 20 μm.

Figs 7–12. Sequence of cortex formation showing alternate formation of three cortical cells per periaxial cell, with the first cortical cell becoming a pseudoperiaxial cell that continues to divide. Scale bars = 10 μm.

Fig. 13. Incomplete cortication in prostrate axis, and rhizoidal cell cut off from periaxial cell, terminating in a digitate tip. Scale bar = 20 μm.

Fig. 14. Erect axis beset with spermatangia. Scale bar = 20 μm.
Fig. 15. Cross section through spermatangial axis (arrow). Scale bar = 10 μm.
Figs 16–17. Tetrasporangial thallus showing tetrasporangia restricted to single node in erect axis. Scale bars = 0.25 mm.
Fig. 18. Cortical node bearing tetrasporangial initials (arrow) produced from periaxial cell. Scale bar = 20 μm.
Fig. 19. Cortical node bearing tetrasporangia closely appressed to contiguous node below. Scale bar = 20 μm.
Fig. 20. Cortical nodes with bulging mature tetrasporangia. Scale bar = 50 μm.
Figs 21–22. Cross-section through cortical node bearing tetrasporangia. Scale bar = 20 μm.
Fig. 23. Acropetal cortical filament at cortical node that bears tetrasporangia. Scale bar = 10 μm.

Figs 24–25. Thallus epiphytic on Hypnea, composed of prostrate axis bearing short erect axes. Scale bars = 0.3 mm (Fig. 24) or 40 μm (Fig. 25).

Fig. 26. Apical region of erect axis. Scale bar = 40 μm.

Figs 27–29. Incomplete cortication in the middle (Fig. 27) and lower (Fig. 28) part of erect axes, and prostrate axis (Fig. 29). Scale bars = 20 μm.

Figs 30–31. Cross-section through upper (Fig. 30) and middle (Fig. 31) part of erect axis showing four periaxial cells per axial cell, and each bearing two cortical cells. Scale bar = 20 μm.

Figs 32–33. Alternate sequence formation of up to three cortical cells per periaxial cell. Scale bar = 5 μm.

Fig. 34. Incomplete cortication in prostrate axis, with rhizoids. Scale bar = 40 μm.

Fig. 35. Cross section through cortical node of prostrate part showing rhizoidal cells cut off from periaxial cell, with digitate tip. Scale bar = 20 μm.

Fig. 36. Male thallus, epiphytic on Hypnea. Scale bar = 0.5 mm.

Figs 37-38. Erect axes bearing spermatothecal clusters at nodes. Scale bar = 20 µm.

Fig. 39. Cross section through node bearing spermatothecal cluster. Scale bar = 10 µm.

Fig. 40. Carpogonophores surrounded by involucral branches. Scale bar = 50 µm.

Fig. 41. Erect axis bearing young carpogonophore. Scale bar = 100 µm.

Fig. 42. Mature carpogonophore. Scale bar = 100 µm.

Fig. 43. Tetrasporangial thallus. Scale bar = 2.5 µm.

Fig. 44. Cortical nodes with tetrasporangial initials (arrows) cut off from periaxial cell, partially covered by acropetal cortical filaments. Scale bar = 20 µm.

Fig. 45. Cortical nodes with two mature tetrasporangia produced from a single periaxial cell. Scale bar = 20 µm.

Fig. 46. Close-up of acropetal cortical filament at tetrasporangial-bearing cortical node. Scale bar = 10 µm.
Figs 47–55. Topotype material (PB-A. No. 845: slides 1, 2, 5) of *Ceramium hamnion codii* Richards from Bermuda.

**Fig. 47.** Thallus epiphytic on *Codium tomentosum*. Scale bar = 0.25 mm.

**Fig. 48.** Vegetative thallus showing erect axes, and rhizoids produced from the cortical nodes in a prostrate axis. Scale bar = 0.25 mm.

**Fig. 49.** Incomplete cortication in the middle part of an erect axis. Scale bar = 20 μm.

**Figs 50–51.** Incomplete cortication in prostrate axis showing two (Fig. 50) or three (Fig. 51, arrows) cortical initials produced from a periaxial cell. Scale bars = 20 μm.

**Fig. 52.** Erect axes bearing spermatangial clusters at the nodes. Scale bar = 40 μm.

**Fig. 53.** Tetrasporangial thallus. Scale bar = 50 μm.

**Figs 54–55.** Cortical nodes with one (Fig. 54) or two tetrasporangia (Fig. 55) produced from a single periaxial cell. Scale bars = 20 μm.

**REPRESENTATIVE SPECIMENS FROM FLORIDA:** epiphytic and co-occurring with *C. repressus* on *Hympoa spinella*, in the drift, Missouri Key–Ohio Key Channel, Florida Keys, FL, USA. coll. T. O. Cho and B. Y. Won; 31 x, 04. LAF-31.10.2004-1-1 (TC999-1).

**HABIT AND ANATOMY:** Thalli are delicate and 0.3–0.6 mm high, consisting of prostrate axes bearing short determinate erect axes growing epiphytically on *Hympoa spinella* (Fig. 24) and *Codium tomentosum* (Fig. 47). Apices are straight and unbranched (Figs 24–26, 48). Erect axes are unilaterally produced from periaxial cells on the dorsal side of the prostrate thallus (Figs 24–25, 48). Axial cells are spherical to cylindrical, reaching 49 ± 5 μm × 16 ± 2 μm (L × W) at the level of the seventh cell away from the apex.

Four periaxial cells are cut off obliquely from the upper part of each parent axial cell (Fig. 30) and remain at the nodes after axial cell elongation (Fig. 31). All periaxial cells produce up to three cortical cells contributing to the cortex. Usually two or three cortical cells are cut off from each periaxial cell in an alternate sequence (Figs 32, 33). The first two are acroetal, cut off obliquely from the upper end (Fig. 32), while the remaining one is basipetal, produced horizontally from the lower end (Fig. 33). Whereas in prostrate axes two (Fig. 50) or three (Figs 29, 51) cortical cells are cut off from each periaxial cell, in most erect axes each periaxial cell cuts off two cortical cells (Figs 26–28, 49). Cortical cells do not divide further into corticating filaments (Figs 26–29) so that acroetal cortication in erect axes remains one-celled, while basipetal cortication is either absent or one-celled. Acroetal cortical cells are ovoid in shape, and basipetal cortical cells are flat (Figs 33, 51, arrows). The cortex is incomplete and banded (Figs 26–29, 49–51), reaching 15 ± 2 μm × 22 ± 6 μm (L × W) at the level of the seventh nodes away from the apex.

Rhizoids are produced singly from periaxial cells at nearly every node on the ventral side of the prostrate axes (Figs 34–
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Table 1. Comparison of morphological features among pertinent creeping *Ceramium* species; ‘—’ means no information is available.

<table>
<thead>
<tr>
<th>Species</th>
<th>Branching at apex of upright</th>
<th>No. of periaxial cells</th>
<th>Pseudo periaxial cell initials from periaxial cell</th>
<th>Diameter of node in upright axis (μm)</th>
<th>Shape of rhizoid</th>
<th>No. of tetrasporangia per parent cell</th>
<th>Division mode of tetrasporangia</th>
<th>Distribution of sporangia</th>
<th>Distribution</th>
<th>Pertinent references</th>
</tr>
</thead>
<tbody>
<tr>
<td><em>C. reptans</em> sp. nov.</td>
<td>straight</td>
<td>5</td>
<td>present</td>
<td>43 ± 5</td>
<td>rod-shaped with pad</td>
<td>1</td>
<td>cruciate</td>
<td>whorled at single node</td>
<td>Florida Keys</td>
<td>this study</td>
</tr>
<tr>
<td><em>C. codii</em> (Richards) Marzoyer</td>
<td>straight</td>
<td>4</td>
<td>absent</td>
<td>22 ± 6</td>
<td>rod-shaped with or without pad inflated</td>
<td>2</td>
<td>tetrahedral</td>
<td>whorled at two nodes</td>
<td>Bermuda, Florida Keys</td>
<td>this study Richards (1901)</td>
</tr>
<tr>
<td><em>C. bisporum</em> Ballantine</td>
<td>rarely branched</td>
<td>4</td>
<td>absent</td>
<td>30</td>
<td>only bisporangia</td>
<td>—</td>
<td>—</td>
<td>single at node</td>
<td>Caribbean</td>
<td>Ballantine (1990)</td>
</tr>
<tr>
<td><em>C. cingulatum</em> Weber-van Bosse</td>
<td>pseudodichotomous</td>
<td>—</td>
<td>absent</td>
<td>80-100</td>
<td>rod-shaped</td>
<td>—</td>
<td>only bisporangia</td>
<td>whorled at most nodes</td>
<td>Indian Ocean</td>
<td>Weber-van Bosse (1923); Cormaci &amp; Furnari (1991); Menceses (1995); Abbott (1999)</td>
</tr>
<tr>
<td><em>C. cingulatum</em> Munces</td>
<td>pseudodichotomous</td>
<td>7-8</td>
<td>absent</td>
<td>42-52</td>
<td>rod-shaped with pad</td>
<td>—</td>
<td>—</td>
<td>whorled at most nodes</td>
<td>North Pacific Mediterranean Sea</td>
<td>Cormaci <em>et al.</em> (1994)</td>
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<td><em>C. incoscum</em> Zanardini</td>
<td>straight</td>
<td>—</td>
<td>absent</td>
<td>100</td>
<td>—</td>
<td>—</td>
<td>tetrahedral</td>
<td>whorled</td>
<td>Puerto Rico, Hawaii</td>
<td>Diaz-Piferer (1968); Ballantine &amp; Wynne (1986); Abbott (1999)</td>
</tr>
<tr>
<td><em>C. procumbens</em> Setchell &amp; Gardner</td>
<td>straight</td>
<td>4</td>
<td>absent</td>
<td>—</td>
<td>rod-shaped with pad</td>
<td>1</td>
<td>cruciate</td>
<td>whorled on several nodes</td>
<td>North Pacific</td>
<td>Setchell &amp; Gardner (1924); Cho <em>et al.</em> (2001)</td>
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<tr>
<td><em>C. punctiforme</em> Setchell</td>
<td>rarely branched</td>
<td>5</td>
<td>absent</td>
<td>50</td>
<td>rod-shaped with pad</td>
<td>—</td>
<td>—</td>
<td>1-4 at 3-5 nodes</td>
<td>North Pacific</td>
<td>Setchell &amp; Gardner (1924); Abbott (1999)</td>
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<tr>
<td><em>C. serpens</em> Setchell &amp; Gardner</td>
<td>rarely branched</td>
<td>4</td>
<td>absent</td>
<td>40-80</td>
<td>rod-shaped with pad</td>
<td>1</td>
<td>—</td>
<td>single at several nodes</td>
<td>North Pacific</td>
<td>Setchell &amp; Gardner (1924); Abbott (1999)</td>
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<tr>
<td><em>Ceramium</em> sp. [= <em>C. tenerre</em> minum (Mertens) Okanuran var brevicornutum (H.E. Peterson) G. Feldmann f. repens f. nov, med Coppejans]</td>
<td>rarely branched</td>
<td>—</td>
<td>absent</td>
<td>50-60</td>
<td>rod-shaped with pad</td>
<td>—</td>
<td>—</td>
<td>clusters of parapsorangi at tip</td>
<td>Mediterranean</td>
<td>Coppejans (1977, 1983)</td>
</tr>
</tbody>
</table>
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35), and are rod-shaped and straight (Fig. 48) or terminate in a 3–4 celled multicellular pad (Figs 34–35) depending on the host.

REPRODUCTIVE STRUCTURES: In male plants, spermatangia are borne in whorls surrounding several cortical nodes of the erect axes (Figs 36–37, 52). Spermatangial parent cells develop from cortical cells and produce 1–2 spermatangia terminally (Figs 38, 39). Spermatangia are colourless and elliptical to spherical, measuring $2 \pm 1 \times 2 \pm 1 \mu$m in size.

In female plants, a single carposporophyte is borne on the upper part of erect axis (Figs 40, 41) and is surrounded by 3–4 finger-like involucral branchlets with incomplete cortication (Figs 40, 42). Mature carposporophytes are spherical, 94 ± 8 μm long and 88 ± 6 μm in diameter.

In tetrasporic plants, tetrasporangia are distributed along several upper cortical nodes of the erect axis (Figs 43, 53). One to two tetrasporangia (Figs 44, 45, 54, 55) develop from a single periaxial cell only. The acropetal cortical cells at the cortical node bearing the tetrasporangia divide, resulting in branched cortical filaments (Fig. 46) partially covering the tetrasporangia (Figs 44, 45). Tetrasporangia are tetrahedrally divided, spherical to ellipsoidal, and average 34 ± 2 μm × 31 ± 1 μm excluding the sheath and 38 ± 1 μm × 37 ± 2 μm with the sheath.

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In tetrasporic plants, tetrasporangia are distributed along several upper cortical nodes of the erect axis (Figs 43, 53). One to two tetrasporangia (Figs 44, 45, 54, 55) develop from a single periaxial cell only. The acropetal cortical cells at the cortical node bearing the tetrasporangia divide, resulting in branched cortical filaments (Fig. 46) partially covering the tetrasporangia (Figs 44, 45). Tetrasporangia are tetrahedrally divided, spherical to ellipsoidal, and average $34 \pm 2 \mu m \times 31 \pm 1 \mu m$ excluding the sheath and $38 \pm 1 \mu m \times 37 \pm 2 \mu m$ with the sheath.

**DISCUSSION**

*Ceriumum reptans* is newly described from the Florida Keys, USA, and *C. codii* is recircumscribed and newly recorded for Florida. Whereas both species share a prostrate axis producing unilateral upright axes dorsally, *C. reptans* sp. nov. has five periaxial cells at each node, a pseudoperiaxial cell nested between each periaxial cell, and cruciately tetrasporangia restricted to a single node appressed to the contiguous lower node. *Ceriumum codii* can be distinguished by four periaxial cells, 1–2 tetrahedrally divided tetrasporangia produced per periaxial cell, and three cortical cells cut off per periaxial cell on the prostrate axis, with the basipetal cortical cell cut off horizontally. Although the new species resembles *C. bisporum* described from Puerto Rico, Caribbean Sea, in possessing prostrate axes bearing unilateral upright axes, *C. bisporum* is characterized by a highly expanded succate rhizoid and occasional erect axes forming laterals (Ballantine 1990).

Among the previously described *Ceriumum* species having the prostrate axis producing upright axes, none has the characteristic transformed cortical cells, termed pseudoperiaxial cells *sensu* Womersley (1978), in their cortical nodes (Table 1). This feature clearly separates *C. reptans* from all other creeping species. The presence and arrangement of pseudoperiaxial cells has been a useful character to define other incompletely corticated *Ceriumum* species (Womersley 1978; Abbott 1999; Cho et al. 2002): *C. australis* Sonder, *C. macilentum* J. Argard, *C. shepherdii* Womersley, *C. clarionense* Setchell & Gardner, and *C. recticorticum* Dawson. Further comparison shows that *C. reptans* is also distinguished from all other species in that it has whorled tetrasporangia borne on only one node of the upright axis, a single cortical node bearing tetrasporangia that is closely appressed to the node below, and tetrasporangia bulging from the cortical bands.

*Ceriumum codii* is distinct from most other creeping *Ceriumum* species in having an unbranched erect axis and apex, two acropetal and one basipetal cortical cells cut off per periaxial cell especially on the prostrate axis, and two tetrasporangia produced from a single periaxial cell (Table 1). The name *C. codii* should be restricted to these taxa characterized by these features that are present in topotype material from Bermuda.

*Ceriumum codii* may not be as widespread a species as is widely reported in the literature, and may comprise several distinct entities (Coppejans 1977). Phylogenetic analyses inferred from DNA sequences are needed to assess whether or not species worldwide going under the name *C. codii* (e.g. Noda 1967; Iwasund 1970; Itano 1972; Lawson & John 1982; Cribb, 1983; Athanasiadis 1987; Millar 1990; Abbott 1999) are conspecific with the material from Bermuda and the Florida Keys, and whether or not the creeping *Ceriumum* species worldwide form a monophyletic group.

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