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 periaxial cells per axial cell; three cortical cells cut off per periaxial cell, with the first acropetal cortical cell becoming the pseudoperiaxial cell that extends longitudinally parallel to the level of neighboring periaxial cells, a second acropetal and third basipetal horizontal cortical cell; and cruciately divided tetrasporangia in whorls bulging from a single node appressed 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 periaxial cells per axial cell, three cortical cells cut off per periaxial cell with the basipetal cortical cell cut off horizontally on the prostrate axis, and 1–2 tetrahedrally divided tetrasporangia produced per periaxial cell. Among the described creeping *Ceramium* species; *C. codii, C. bisporum, C. cingulatum, C. cingulum, C. dorsiventrale, C. incospicuum, C. jolyi, C. luetzelburgii, C. procumbens, C. poeppigianum, C. punctiforme, C. serpens*, and *C. tenerrimum* var. *brevizonatum* f. *repens*, none has the characteristic pseudoperiaxial 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 pseudodichotomous branching or by prostrate axes bearing erect axes. Female gametophytes produce cystocarps surrounded by fingerlike involucral branches, male thalli have spermatangia produced first on the adaxial side and later in whorls along the axis, and tetrasporophytes bear tetrasporangia cut off from periaxial 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* (Díaz-Piferrer) 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. incospicuum* Zanardini (1839, p. 136) from the Mediterranean Sea (Cormaci *et al.* 1994, p. 1001); *C. luetzelburgii* Schmidt (1924, p. 98) described from Brazil; *C. poeppigianum* Grunow (1867, p. 64) described from E 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. punctiforme* Setchell (1924, p. 158) described from the Gulf of California; *C. serpens* Setchell & Gardner (1924, p. 775) described from the Gulf of California; and *Ceramium* sp. reported from the Mediterranean [Coppejans 1977; as *C. tenerrimum* (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 (Itono 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; Díaz-Piferrer 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).

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Two creeping *Ceramium* species comprising predominantly prostrate axes bearing unilateral, 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-occurring epiphytically on several individuals of the same host, *Hypnea 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*, exciccata #1899, Phycotheca Boreali-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 Ie 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 minuti, epiphytici in *Hypnea spinella*, constantes ex parte prostrata axe horizontali dorsaliter ramos adventitios unilaterales erectos ventraliter rhizoidea producenti; axes erecti uniseriati extensi 0.8–1.2 mm; apices recti; rhizoidea brevia disco 3–4 cellulari digitato; corticatio incompleta, constans ex 3 vel 4 seriebus cellularum; cellulae periaxiales 5; spermatangia ad apices ramorum erectorum cellulis parentalibus spermatangiorum in cellulis corticalibus extimis exorientibus; tetrasporangia cruciata solum ad nodum unicum ramorum erectorum exorientia, singulatim in quoque cellula periaxiali formata, protrudentia e nodo corticali 3–6 segmentis infra apicem, 38–42 μm diam., in verticillis.

Thalli minute, epiphytic on *Hypnea spinella*, consisting of a prostrate portion with a horizontal axis adventitiously producing unilateral 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 digitate pad; cortication incomplete, consisting of 3–4 cell rows; periaxial cells 5 in number, each cutting off 2 ovoid acropetal and 1 flattened basipetal cortical cell, with the first cortical cell becoming the pseudoperiaxial cell that continues to divide, growing parallel to and extending to the level of neighboring periaxial cells; spermatangial clusters near apices of upright branches, spermatangial parent cells borne on the outermost cortical cells; tetrasporangia restricted to a single node of the upright branches, with a single tetrasporangial initial cut off per periaxial cell, protruding from a cortical node 3–6 segments below apex, cruciately divided, 38–42 μm in diameter, in whorls.

HOLOTYPE (designated here): Fig. 16, tetrasporophyte, LAF-31.10.2004-1-2 (TC999-2), epiphytic and co-occurring with *C. codii* on *Hypnea spinella*, in the drift, Missouri Key–Ohio Key Channel, Florida Keys, FL, USA, coll. T.O. Cho and B.Y. Won; 31. x. 04. Additional isotypes: LAF-31.10.2004-1-2, tetrasporophytes, male gametophytes, and vegetative thalli.

ETYMOLOGY: The species is named for the creeping habit and characteristic pseudoperiaxial 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 periaxial 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 periaxial 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 periaxial 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 periaxial cells, which it resembles, and becomes a pseudoperiaxial cell (Figs 8, 9) that continues to divide. Whereas a single pseudoperiaxial cell is located on one side of each periaxial cell (Fig. 4), the first-formed periaxial cell bears two pseudoperiaxial cells bilaterally (Figs 6, 12). The third cortical cell is cut off horizontally from the lower end of each periaxial 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 node 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 periaxial 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). Spermatangia are organized in whorls surrounding several nodes of the erect axes (Fig. 15). Spermatangia are colourless and elliptical to spherical, measuring $2 \pm 1 \times 2 \pm 1$ μm in size.

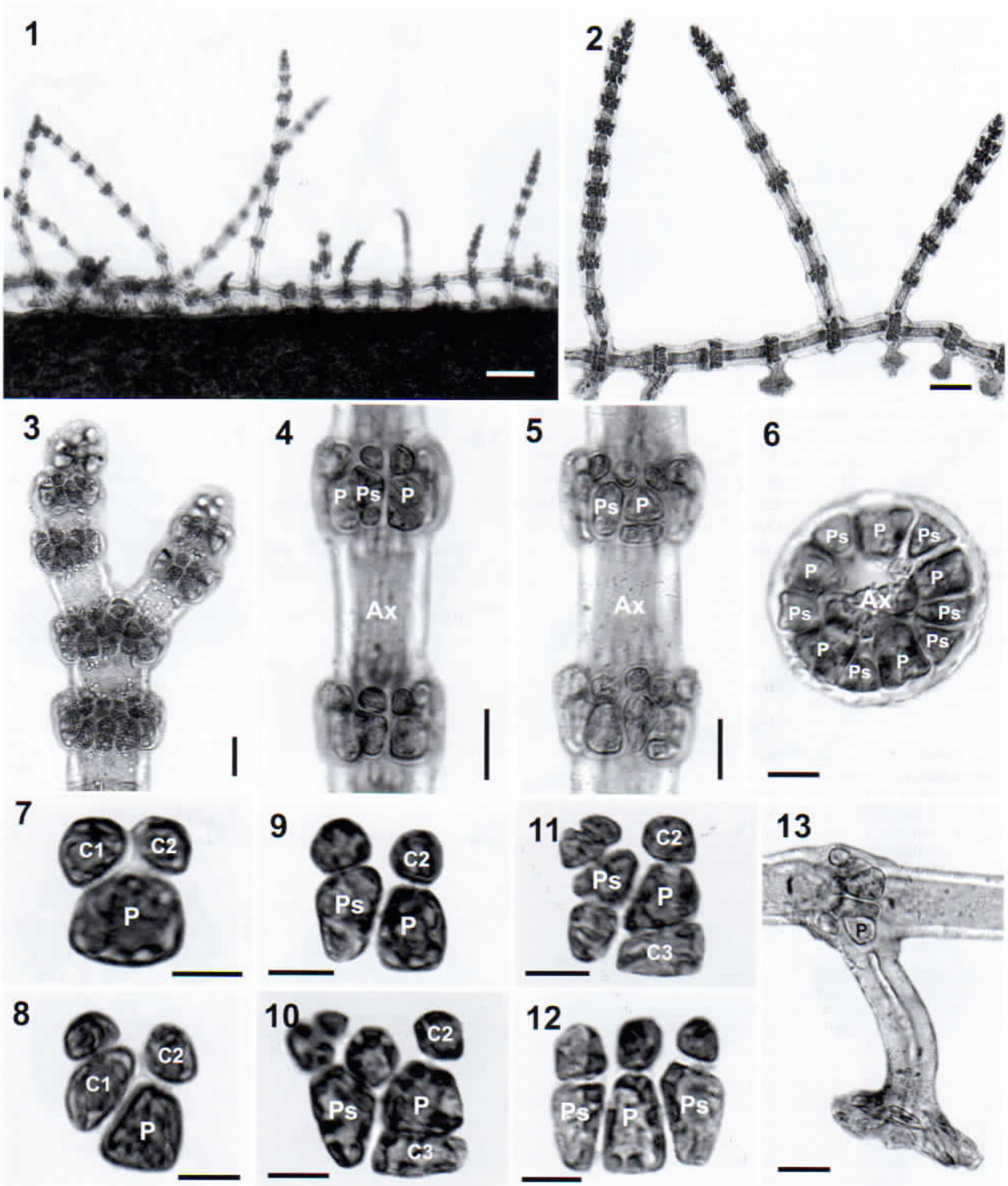
In tetrasporic plants, tetrasporangia are restricted to a single node, 3–6 segments below the apex of the erect axis (Figs 16, 17). A single tetrasporangium is cut off per periaxial cell (Figs 18, 19). Tetrasporangia are produced in an alternate sequence resulting in a whorl around the axis (Figs 20–22). 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

TOPOTYPE: Figs. 47–55; exciccata nr. 1899, as *Ceramothamnion codii* Richards, Phycotheca Boreali-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' (LAF!).



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).

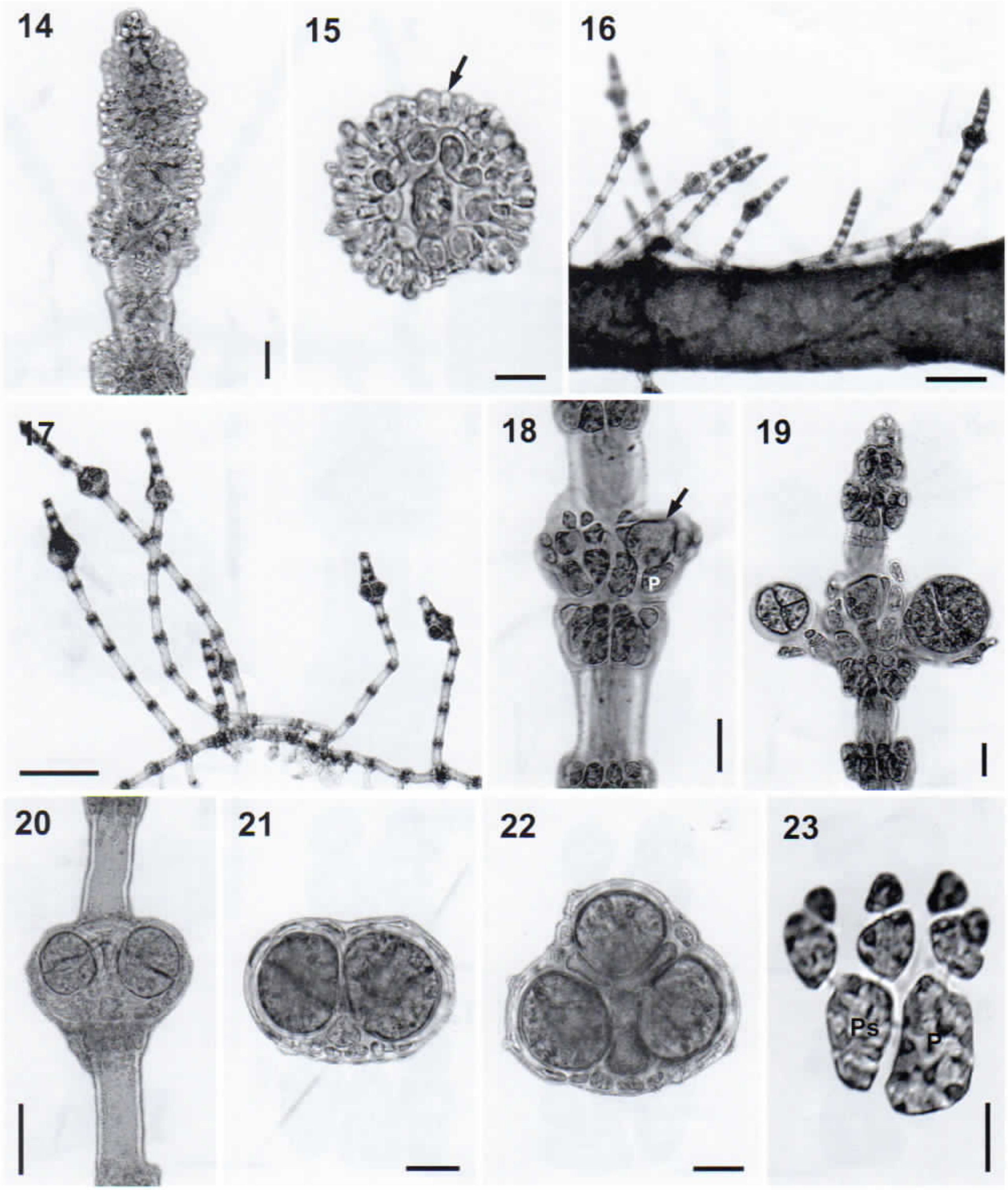
Fig. 3. Apical region of prostrate axis showing pseudodichotomous branching pattern. Scale bar = 20 μm.

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.



Figs 14–23. Reproductive structures (LAF-31-10-2004-1-2: slides 3, 5, 6) of *Ceramium reptans* T.O. Cho & S. Fredericq.

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.

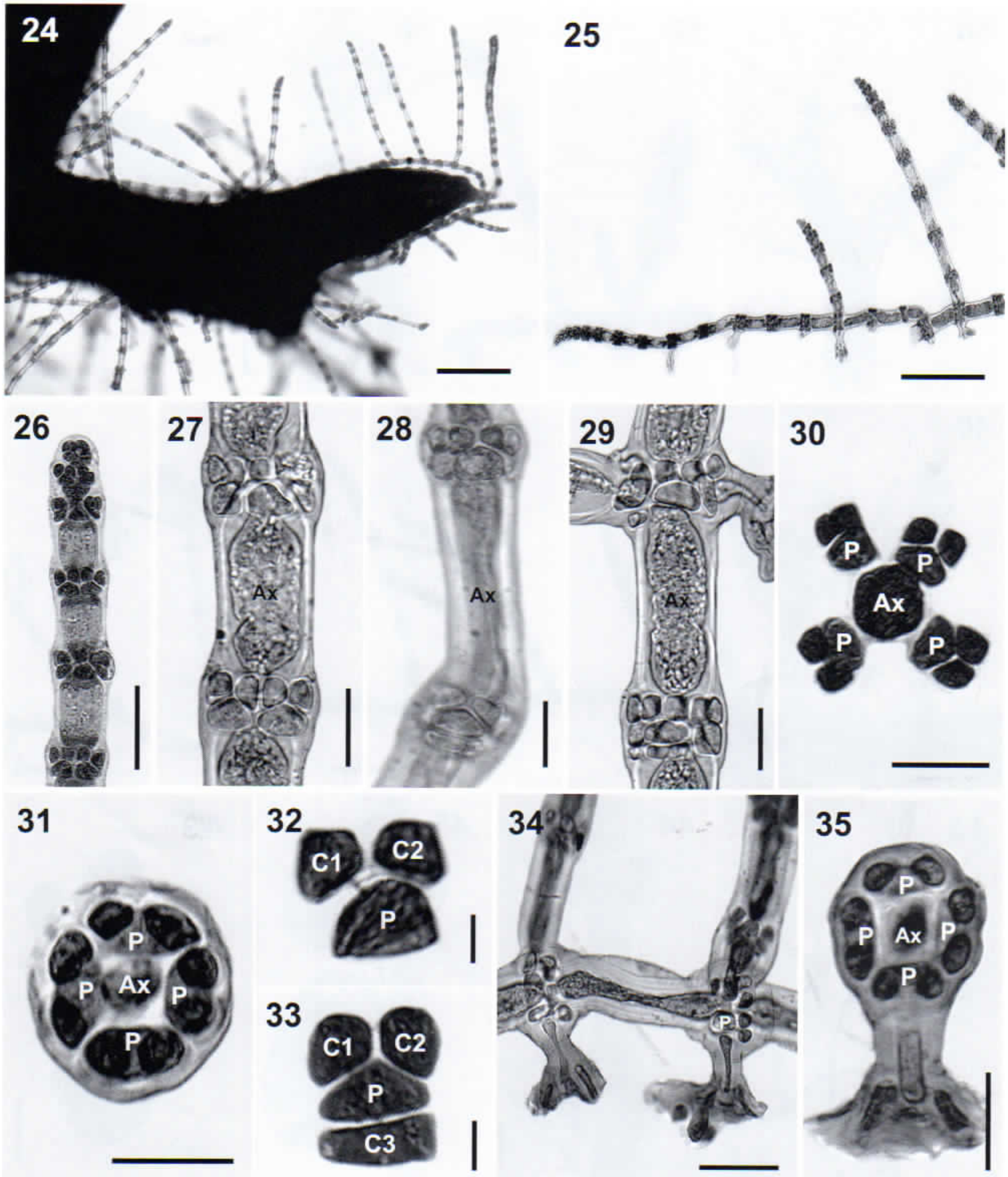
Fig. 18. Cortical node bearing tetrasporangial initials (arrow) produced from periaxial cell. Scale bar = 20 μm.

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 24–35. Vegetative structures (LAF-31-10-2004-1-1: slides 1–5) of *Ceramium codii* (Richards) Mazoyer.

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.

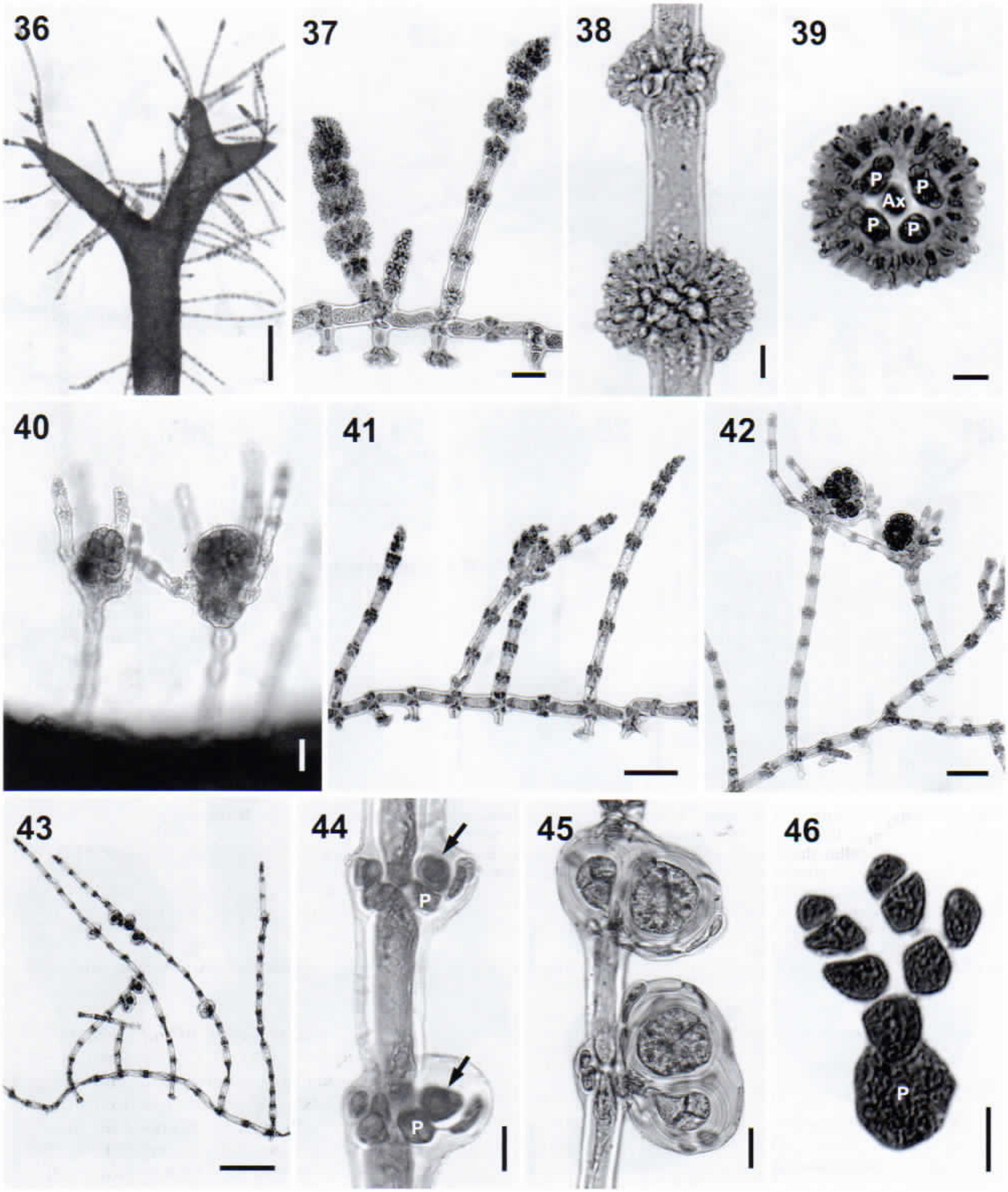
Figs 27–29. Incomplete cortication in the middle (Fig. 27) and lower (Fig. 28) part of erect axes, and prostrate axis (Fig. 29). Scale bars = 20 μm.

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.



Figs 36–46. Reproductive structures (LAF-31-10-2004-1-1: slides 7–11) of *Ceramium codii* (Richards) Mazoyer.

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

Figs 37–38. Erect axes bearing spermatangial clusters at nodes. Scale bar = 20 μm.

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

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

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

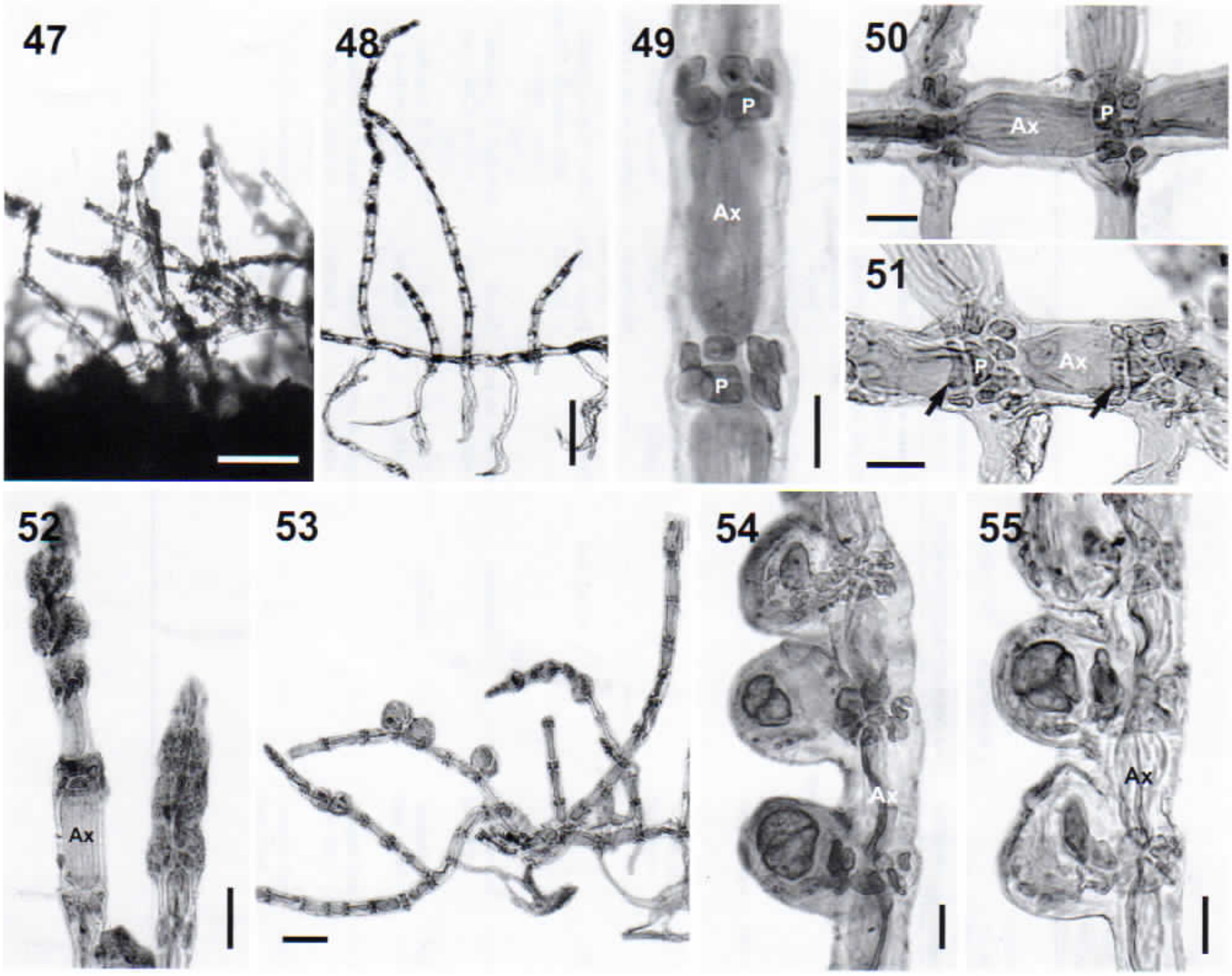
Fig. 42. Mature carposporophyte. Scale bar = 100 μm.

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 (P.B.-A. No. 845: slides 1, 2, 5) of *Ceramothamnion 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. reptans* on *Hypnea 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 *Hypnea 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 acropetal, 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 acropetal cortication in erect axes remains one-celled, while basipetal cortication is either absent or one-celled. Acropetal 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–

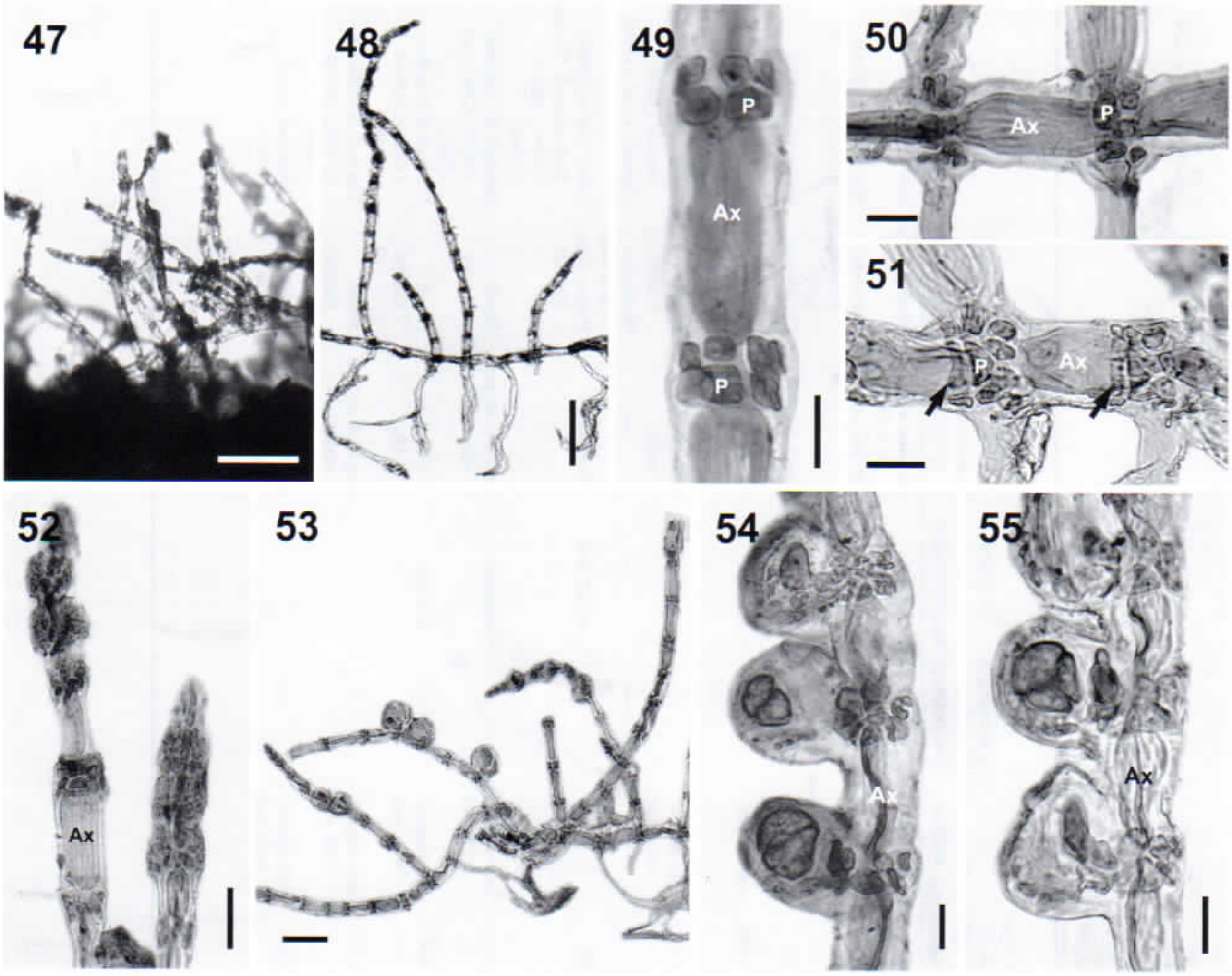


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Fig. 52. Erect axes bearing spermatangial clusters at the nodes. Scale bar = 40 μm.
Fig. 53. Tetrasporangial thallus. Scale bar = 50 μm.
Figs 54–55. Cortical nodes with one (Fig. 54) or two tetrasporangia (Fig. 55) produced from a single periaxial cell. Scale bars = 20 μm.

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Rhizoids are produced singly from periaxial cells at nearly every node on the ventral side of the prostrate axes (Figs 34–

Table 1. Comparison of morphological features among pertinent creeping *Ceramium* species; '—' means no information is available.

	Branching at apex of upright	No. of periaxial cells	Pseudo periaxial cells presence/absence	Cortical cell initials from periaxial cell	Diameter of node in upright axis (μm)	Shape of rhizoid	No. of tetrasporangia per parent cell	Division mode of tetrasporangia	Distribution of sporangia	Distribution	Pertinent references
C. reptans sp. nov.	straight	5	present	2 acropetal; 1 basipetal	43 ± 5	rod-shaped with pad	1	cruciate	whorled at single node	Florida Keys	this study
C. codii (Richards) Mazoyer	straight	4	absent	2 acropetal; 1 basipetal	22 ± 6	rod-shaped with or without pad	2	tetrahedral	two per node	Bermuda, Florida Keys	this study Richards (1901)
C. bisporum Ballantine	rarely branched	4	absent	1 acropetal	30	inflated	only bisporangia	only bisporangia	single at node (bisporangia)	Caribbean	Ballantine (1990)
C. cingulatum Weber-van Bosse	pseudodichotomous	—	absent	2 acropetal; 2 basipetal	80–100	rod-shaped	—	cruciate	whorled at most nodes	Indian Ocean	Weber-van Bosse (1923); Cormaci & Furnari (1991)
C. cingulum Meneses	pseudodichotomous	7–8	absent	2 acropetal; 2 basipetal	42–52	rod-shaped with pad	—	cruciate	whorled at most nodes	North Pacific	Meneses (1995); Abbott (1999)
C. incospicuum Zanardini	straight	—	absent	2 acropetal; 2 basipetal	—	—	—	—	—	Mediterranean Sea	Cormaci *et al.* (1994)
C. jolyi (Díaz-Piferrer) Ballantine & Wynne	straight	4–6	absent	2 acropetal; 2 basipetal	100	—	—	tetrahedral	whorled	Puerto Rico, Hawaii	Díaz-Piferrer (1968); Ballantine & Wynne (1986), Abbott (1999)
C. procumbens Setchell & Gardner	straight	4	absent	2 acropetal; 2 basipetal	—	rod-shaped with pad	1	cruciate	whorled on several nodes	North Pacific	Setchell & Gardner (1924); Cho *et al.* (2001)
C. punctiforme Setchell	rarely branched	5	absent	2 acropetal; 1 basipetal	50	rod-shaped with pad	—	cruciate	1–4 at 3–5 nodes	North Pacific	Setchell & Gardner (1924); Abbott (1999)
C. serpens Setchell & Gardner	rarely branched	4	absent	2 acropetal; 2 basipetal	40–80	rod-shaped with pad	1	—	single at several nodes	North Pacific	Setchell & Gardner (1924), Abbott (1999)
Ceramium sp. [=*C. tenerrimum* (Mertens) Okamura var *brevizonatum* (H.E. Peterson) G. Feldmann f. *repens* f. nov. med Coppejans]	rarely branched	—	absent	2 acropetal; 2 basipetal	50–60	rod-shaped with pad	—	—	clusters of parasporangia at tip	Mediterranean	Coppejans (1977, 1983)

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 $2 \pm 1 \times 2 \pm 1$ μm 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 $\times$ 31 ± 1 μm excluding the sheath and 38 ± 1 μm $\times$ 37 ± 2 μm with the sheath.

DISCUSSION

Ceramium 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. *Ceramium 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 saccate rhizoid and occasional erect axes forming laterals (Ballantine 1990).

Among the previously described *Ceramium* 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 found a useful character to define other incompletely corticated *Ceramium* species (Womersley 1978; Abbott 1999; Cho *et al.* 2002): *C. australe* Sonder, *C. macilentum* J. Agardh, *C. shepherdii* Womersley, *C. clarionense* Setchell & Gardner, and *C. recticortum* 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.

Ceramium codii is distinct from most other creeping *Ceramium* 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.

Ceramium 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; Jaasund 1970; Itono 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 *Ceramium* species worldwide form a monophyletic group.

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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.

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