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Developmental morphology of a poorly documented alga, *Ceramium recticorticum* (Ceramiaceae, Rhodophyta), from the Gulf of California, Mexico

*Tae Oh CHO[a], Rafael RIOSMENA-RODRIGUEZ[b] & Sung Min BOO[a] **

[a]Department of Biology, Chungnam National University, Daejon 305-764, Korea

[b]Programa de Investigación en Botánica Marina, Marine Biology Department, UABCS, Ap. Postal 19-B,

La Paz, B.C.S. 23080, Mexico

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Abstract — We studied the vegetative, reproductive, and developmental morphology of *Ceramium recticorticum* Dawson. Thalli are alternately branched and have four peraxial cells with four to five pseudoperiaxial cells. Acropetal and basipetal cortical cells are produced by transverse division of periaxial and pseudoperiaxial cells and are rectangular, horizontally elongated, and regularly arranged in four to five columns and rows. Spermatangia are produced on the adaxial side of the upper branches and later in whorls. Cystocarps are spherical and surrounded by 2-4 involucral branches. Tetrasporangia are produced in an opposite sequence, completely covered by cortical cells, and arranged in whorls. The development of spermatangia and cystocarps are described for the first time and conform to the description of the genus. *Ceramium recticorticum* is similar to *C. fimbriatum* Setchell *et* Gardner, *C. flaccidum* (Kützing) Ardissone, and *C. gracillimum* (Kützing) Griffiths *et* Harvey *ex* Harvey var. *byssoideum* (Harvey) Mazoyer in sharing a horizontally elongated basipetal cortical cell by transverse division of periaxial cells and rhizoids composed of unicellular filaments with pads produced from periaxial cells. These taxa may be considered as a group of closely related species.

Ceramiaceae / *Ceramium recticorticum* / marine red algae / morphology / taxonomy

Résumé — Morphologie du développement d'un algue peu étudiée, *Ceramium recticorticum* (Ceramiaceae, Rhodophyta), dans le Golfe de Californie (Mexique). Nous avons étudié la morphologie du thalle, de la reproduction et du développement de *Ceramium recticorticum* Dawson. Les thalles ont une ramification alterne et ont quatre cellules périaxiales avec quatre à cinq cellules pseudopériaxiales. Les cellules corticales acropètes et basipètes sont produites par la division transversale des cellules périaxiales et pseudopériaxiales et sont rectangulaires, allongées horizontalement et disposées régulièrement en quatre à cinq colonnes et en rangées. Les spermatocystes sont produits du côté adaxial des derniers verticilles des rameaux supérieurs. Les cystocarpes sont sphériques et entourés par 2-4 rameaux involucraux. Les tétrasporocystes sont produits en séries opposées, complètement recouverts par des cellules corticales et disposés en verticilles. Le développement des

* Correspondence and reprints: smboo@cnu.ac.kr

spermatocystes et des cystocarpes sont décrits pour la première fois et confirment que la description du genre *Ceramium recticorticum* est semblable à celle de *C. fimbriatum* Setchell *et* Gardner, *C. flaccidum* (Kützing) Ardissone et *C. gracillimum* (Kützing) Griffiths *et* Harvey *ex* Harvey var. *byssoideum* (Harvey) Mazoyer en ayant en commun une cellule corticale basipète horizontale produite par la division transversale des cellules périaxiales ainsi que des rhizoïdes composés de filaments unicellulaires avec des bourrelets produits par les cellules périaxiales. Ces taxons doivent être considérés comme un groupe d'espèces voisines. (Traduit par la Rédaction.)

Algues rouges marines / Ceramiaceae / *Ceramium recticorticum* / morphologie / taxinomie

INTRODUCTION

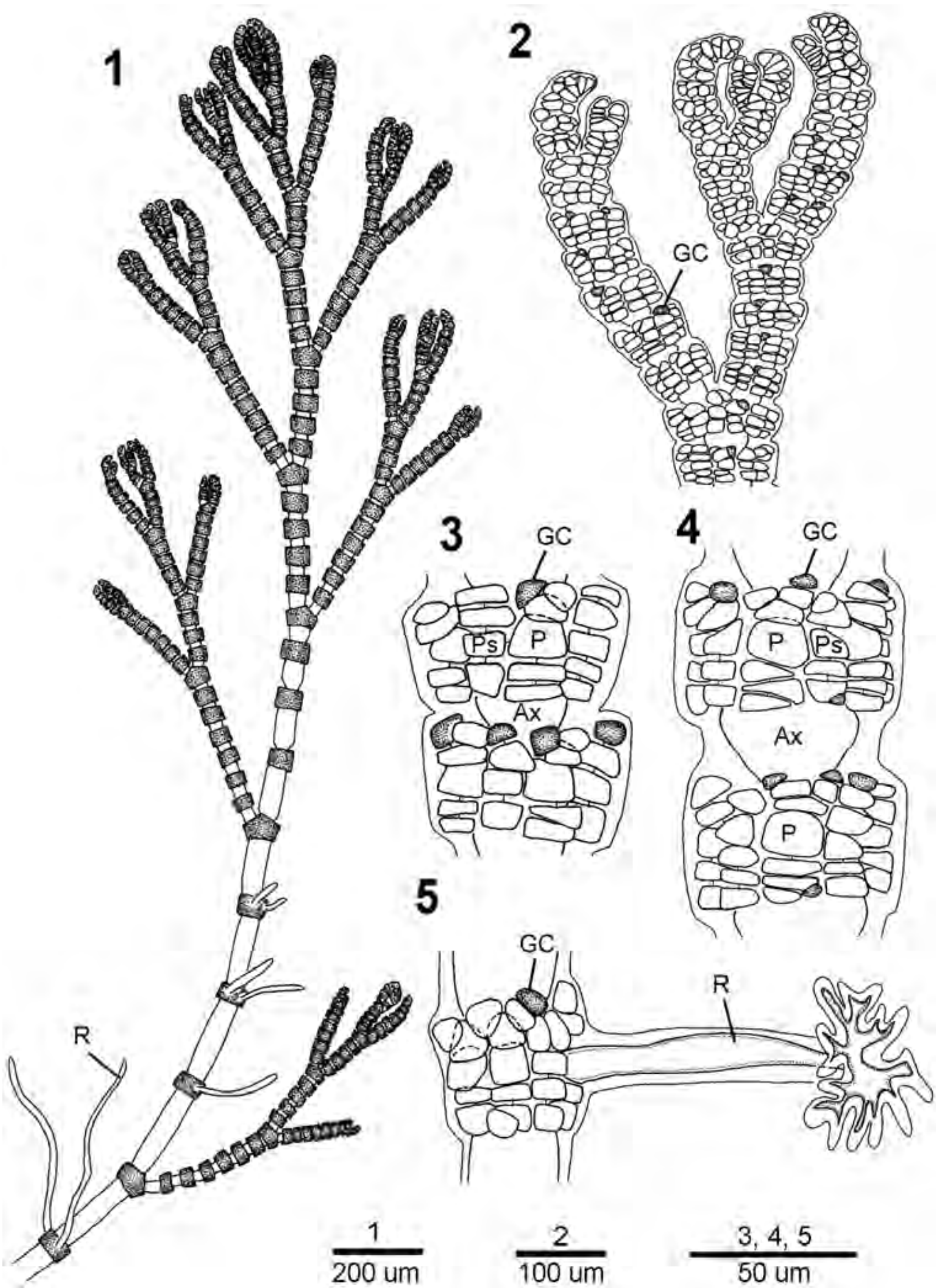
Ceramium Roth is one of the largest genera of Rhodophyta; about 191 species have been listed from tropical to polar seas in both hemispheres (Boo & Lee, 1994). Thalli are characterized vegetatively by cylindrical axial cells incompletely to completely covered by cortical cells and by pseudodichotomous branching. Male thalli have spermatangia produced first on the adaxial side and later in whorls along the axis. Female gametophytes produce cystocarps surrounded by finger-like involucral branches (Miranda, 1929; Hommersand, 1963). Tetrasporangia are produced from periaxial cells or irregularly from cortical cells and are naked or covered by cortical cells (Nakamura, 1965; Womersley, 1978). Some taxonomic and floristic accounts of the Pacific species have been provided (Setchell & Gardner, 1924, 1937; Smith, 1944; Dawson, 1962; Hommersand, 1963; Nakamura, 1965; Abbott & Hollenberg, 1976; Itono, 1977; Abbott, 1999), but there remain several poorly known species from this region. Furthermore, the taxonomy of *Ceramium* at the species level is still in state of some confusion owing to a lack of knowledge pertaining to morphological and anatomical variability (Dixon 1960; Boo & Lee, 1994).

Ceramium recticorticum was originally described by Dawson (1950) from non-gametangial material collected in Bahía Bocochibampo near Guaymas, Sonora, Mexico. Although Dawson (1963) extended its known distribution to the Galapagos Islands, *C. recticorticum* is still poorly documented because male and female thalli had not been collected.

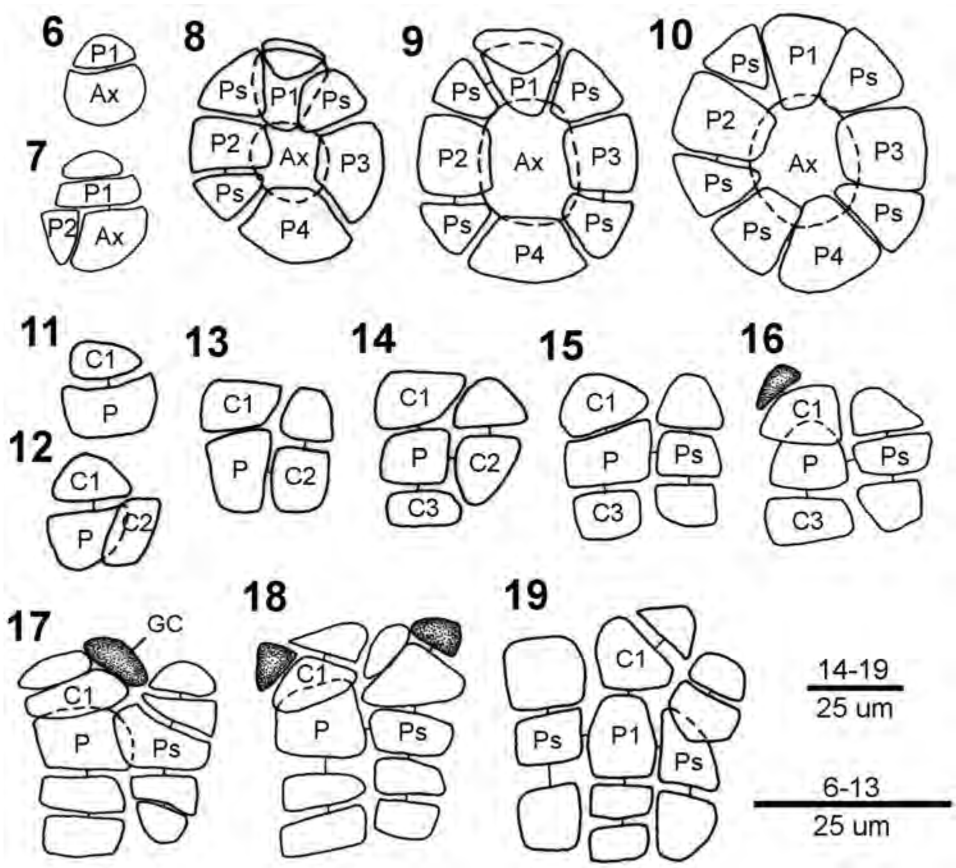
We recently collected *Ceramium recticorticum* in all reproductive stages from a littoral tide pool in the southwestern Gulf of California, Mexico. The goal of this paper is to describe in detail the developmental morphology and anatomy of the vegetative and reproductive structures of *C. recticorticum* and to confirm the taxonomic integrity of the species.

MATERIALS AND METHODS

Specimens of *Ceramium recticorticum* were collected in abundance in the inter- to subtidal zone in the southwestern Gulf of California, Mexico: Balandra, Bahía de La Paz (Cho & Riosmena-Rodriguez, Chungnam National University, Daejon ('CNUK') : C004914, C004930, C004935, C004939, vegetative; C004923-4,



Figs 1-5. *Ceramium recticorticum* Dawson.
Fig. 1. Vegetative thallus. Fig. 2. Apex. Figs 3-4. Detail of cortical nodes showing gland cells (GC), periaxial cell (P), and pseudoperiaxial cell (Ps). Ax = axial cell. Fig. 5. Rhizoid (R) having digitate pad.



Figs 6-19. *Ceramium recticorticum* Dawson.
Figs 6-10. Development of periaxial cells from axial cell. P1, P2, P3, and P4 indicate sequence of periaxial cell formation. Figs 11-19. Development of pseudoperiaxial and cortical cells from periaxial cell. C1, C2, and C3 indicate sequence of cortical cell formation. Other abbreviations as in Figs 1-5.

C004927-8, C004938, cystocarpic; C004909, C004929, tetrasporangial; C004925 C005103, C005105-6, mixed with spermatangial, cystocarpic, and tetrasporangial, 20 May 2000); Punta Perico, Bahía de Muertos (Cho & Riosmena-Rodriguez, CNUK C004854, C004865, C004874, C004879, C004880-1 vegetative, 5 Jun. 2000); South side of Ensenada, Bahía Bocochibampo near Guaymas, Sonora (Isotype in UC and MICH, Dawson 1769a, 16 May 1946); Bahía Bocochibampo near Guaymas, Sonora (paratype in MICH, Dawson 3566, 22 Nov. 1946).

Material was preserved in 4 % formaldehyde/seawater. Microscope observations were made from material stained with 1 % aqueous aniline blue acidified with dilute HCl. Drawings were made with a camera lucida attached to an Olympus microscope (VANOX AHBT3). Our collections were compared with isotype and paratype material from UC and MICH (Holmgren *et al.*, 1990). Herbarium specimens and voucher slides used in this study are deposited in the

Tab. 1. A morphological comparison between *Ceramium recticorticum* and similar species.

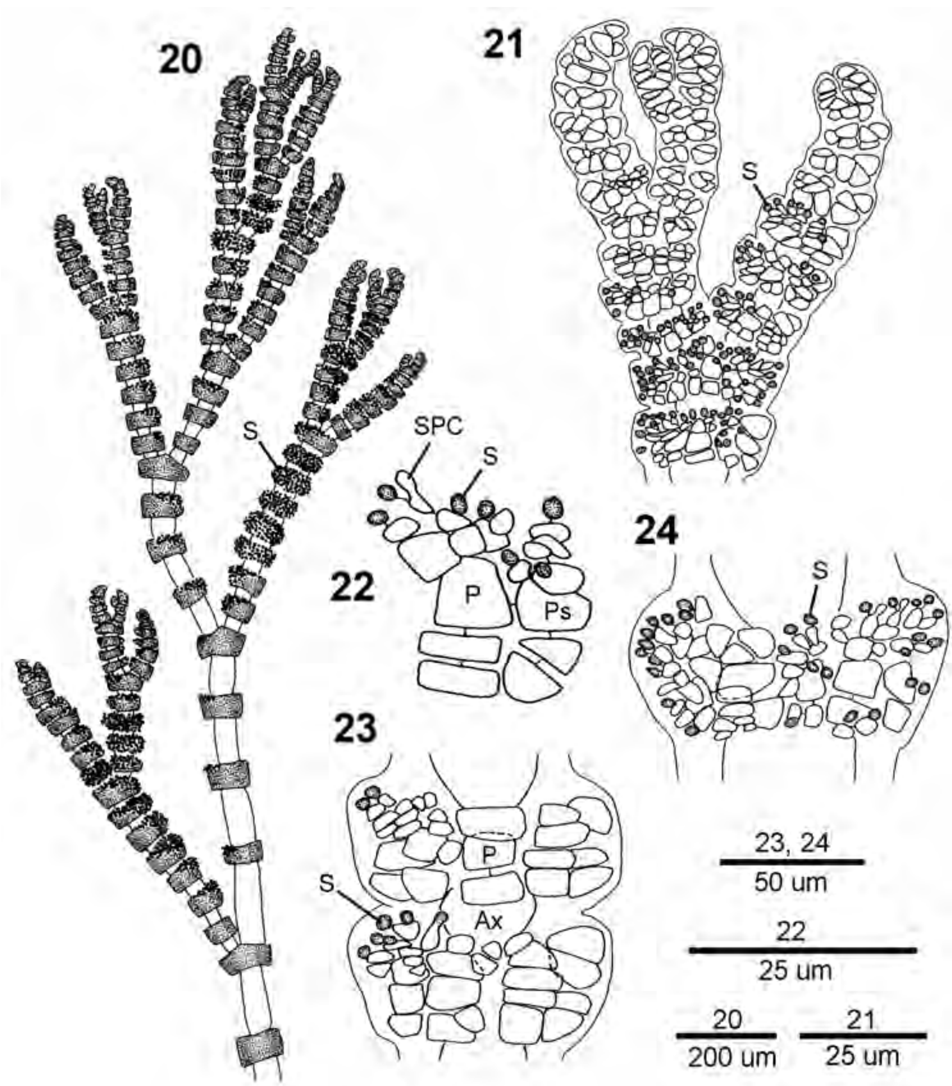
Characters	*C. recticorticum*	*C. gracillimum*	*C. fimbriatum* var. *byssoideum*	*C. flaccidum*
Thallus length (cm)	0.5	0.5	1.0	1.0
Axis width (µm)	50	40-50	100	80
Periaxial cell number	4	4-5	7-8	6-7
Pseudoperiaxial cells	present	absent	absent	absent
Cortical cells formed by transversal division	acropetal & basipetal corticating filaments	basipetal corticating filament	basipetal corticating initial	basipetal corticating initial
Shape of gland cells	spherical	spherical	clavate	spherical
Tetrasporangia diameter (µm)	33 ± 2	–	35	45
Tetrasporangial division	cruciate	–	tetrahedral	tetrahedral
Reference	this study	Dawson (1962) Stegenga & Vroman (1987)	Abbott (1999)	Abbott (1999)

herbarium of CNUK, Daejon, Korea. One to three tufts from every host collected from Balandra, Bahía de La Paz were isolated, and a total of 14 individuals from seven to eight algal tufts were selected in order to measure quantitative characters.

RESULTS

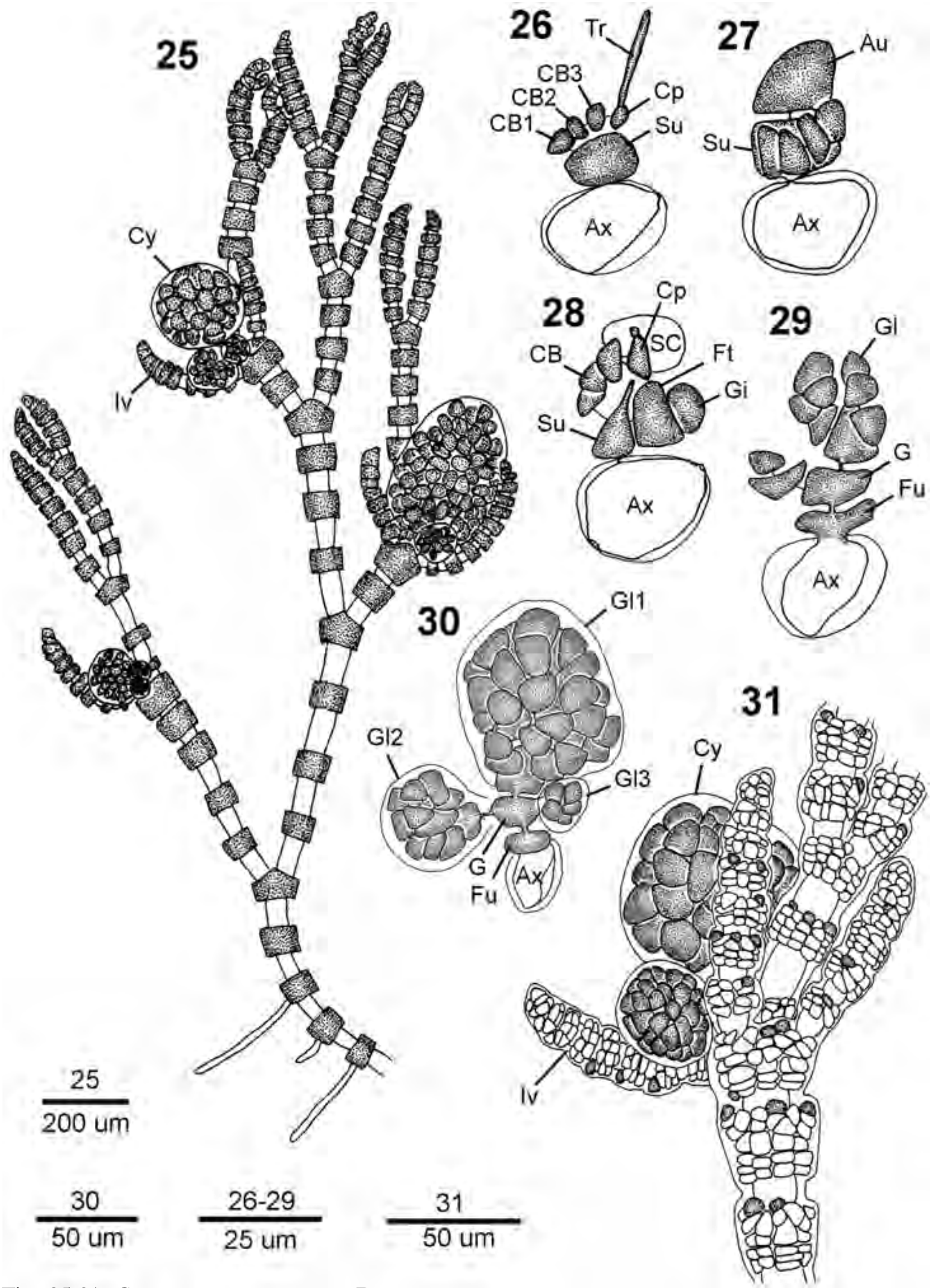
Vegetative structure. Thalli are delicate, brown-red in color, and adhere to paper upon drying. They generally form dense tufts, 0.4 ± 0.1 cm tall (Fig. 1). Thalli consist of erect and prostrate axes anchored to the substratum by rhizoids originating from the basal thallus parts and from prostrate axes. The apical region is slightly incurved (Fig. 2). The erect axes are all composed of an axial cell row and of cortical nodes (Figs 3, 4). The axes are 48 ± 2 µm wide at the level of the fifth branch below the apex. Gland cells, measuring 9 ± 1 µm long × 11 ± 1 µm in diameter, are spherical to ovoid, are produced by the oblique division of terminal cells of the acropetally or basipetally corticating filaments, and are dispersed along the axis (Figs 2-4).

Branches are typically alternate, unequal, and in a same plane (Fig. 1). When a branch is produced, the apical cell first divides obliquely. The apical initial on the adaxial side functions as the apical cell of the main branch. Branches are produced at intervals of four or five segments along the main branches, and of five to seven segments in the lateral branches. Occasionally, adventitious branches are produced from periaxial cells in the lower thallus part that are small and curved. Axial cells are produced by slightly oblique division of the apical cells, spherical to cylindrical, and 196 ± 30 µm long by 39 ± 5 µm in diameter midway in the fifth branch segment below the apex, resulting in a L:W ratio of about 5:1.

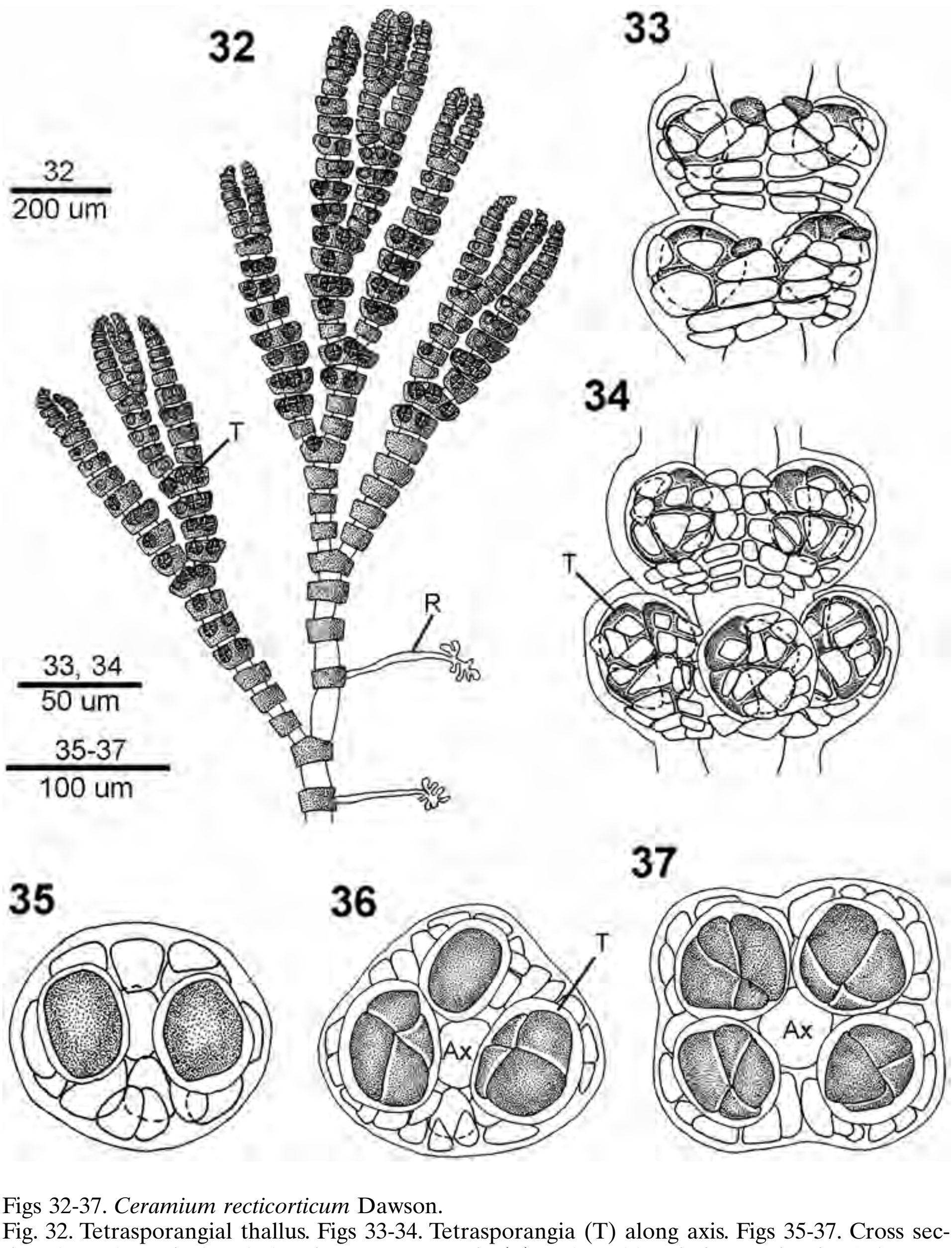


Figs 20-24. *Ceramium recticorticum* Dawson.
Fig. 20. Male thallus. Fig. 21. Apex with spermatangia (S). Fig. 22. Spermatangia developed from spermatangial parent cell (SPC). Fig. 23. Spermatangia on adaxial face. Fig. 24. Spermatangia in whorl. Other abbreviations as in Figs 1-5.

Four periaxial cells are cut off obliquely from the upper part of each parent axial cell (Figs 6-10) and remain at the node after axial cell elongation. The first periaxial cell is produced on the abaxial side of the 2nd or 3rd axial cell below apex (Fig. 6). The remaining three periaxial cells are then cut off in an alternating sequence, first to one and then to the other side of the first periaxial cell, with the fourth cell borne at the abaxial side (Figs 7-10).



Figs 25-31. *Ceramium recticorticum* Dawson.
Fig. 25. Female thallus. Fig. 26. Procarp composed of carpogonial branch (CB) and carpogonium (Cp). CB1, CB2, and CB3 indicate sequence formation, Su = supporting cell, Tr = trichogyne. Fig. 27. Development of auxiliary cell (Au) from supporting cell. Fig. 28. Development of gonimoblast initial (Gi) and foot cell (Ft) from auxiliary cell. SC = sterile cell. Fig. 29. Development of gonimolobes (Gl) from gonimoblast (G). Fu= fusion cell. Fig. 30. Three gonimolobes. Gl1, Gl2, and Gl3 indicate sequence formation. Fig. 31. Mature cystocarps (Cy) surrounded by involucral branches (Iv). Other abbreviations as in Figs 1-5.



Figs 32-37. *Ceramium recticorticum* Dawson.
Fig. 32. Tetrasporangial thallus. Figs 33-34. Tetrasporangia (T) along axis. Figs 35-37. Cross section through cortical node bearing tetrasporangia (T). Other abbreviations as in Figs 1-5.

All periaxial cells produce corticating filaments that form the cortex. The mature cortex is incomplete, covering the axial cells only at the nodes (Figs 3, 4). The first corticating initial is cut off transversely from the anterior end and produces cortical cells acropetally (Fig. 11). The second is cut off longitudinally on the adaxial side of a periaxial cell (Figs 12-13) and forms a pseudoperiaxial cell (Figs 15, 16) that is located between periaxial cells (Fig. 10). The third is cut off transversely from the posterior end (Fig. 14) and produces cortical cells basipetally (Figs 17, 18). However, only the first-formed periaxial cell forms four corticating initials in an alternating sequence, and two of which become pseudoperiaxial cells (Fig. 19). The other periaxial cells form only three corticating initials in a circle (Fig. 18). Each corticating initial produces one or two cortical cells or a gland cell. Ascending and descending files from periaxial and pseudoperiaxial cells have lineages in which the cells are rectangular and horizontally elongated (Figs 17-19). Three vertical rows of corticating filaments are usually produced from the first-formed periaxial cell (Fig. 19), while two vertical rows of corticating filaments are formed from the other periaxial cells (Fig. 18). Thus, a total of nine vertical rows of corticating filaments arise from four periaxial cells at each cortical node, with four or five vertical rows of cells visible from one side (Figs 3, 4). Most of the cortical cells are rectangular, horizontally elongated, and regularly arranged in horizontal and vertical rows (Figs 17, 18).

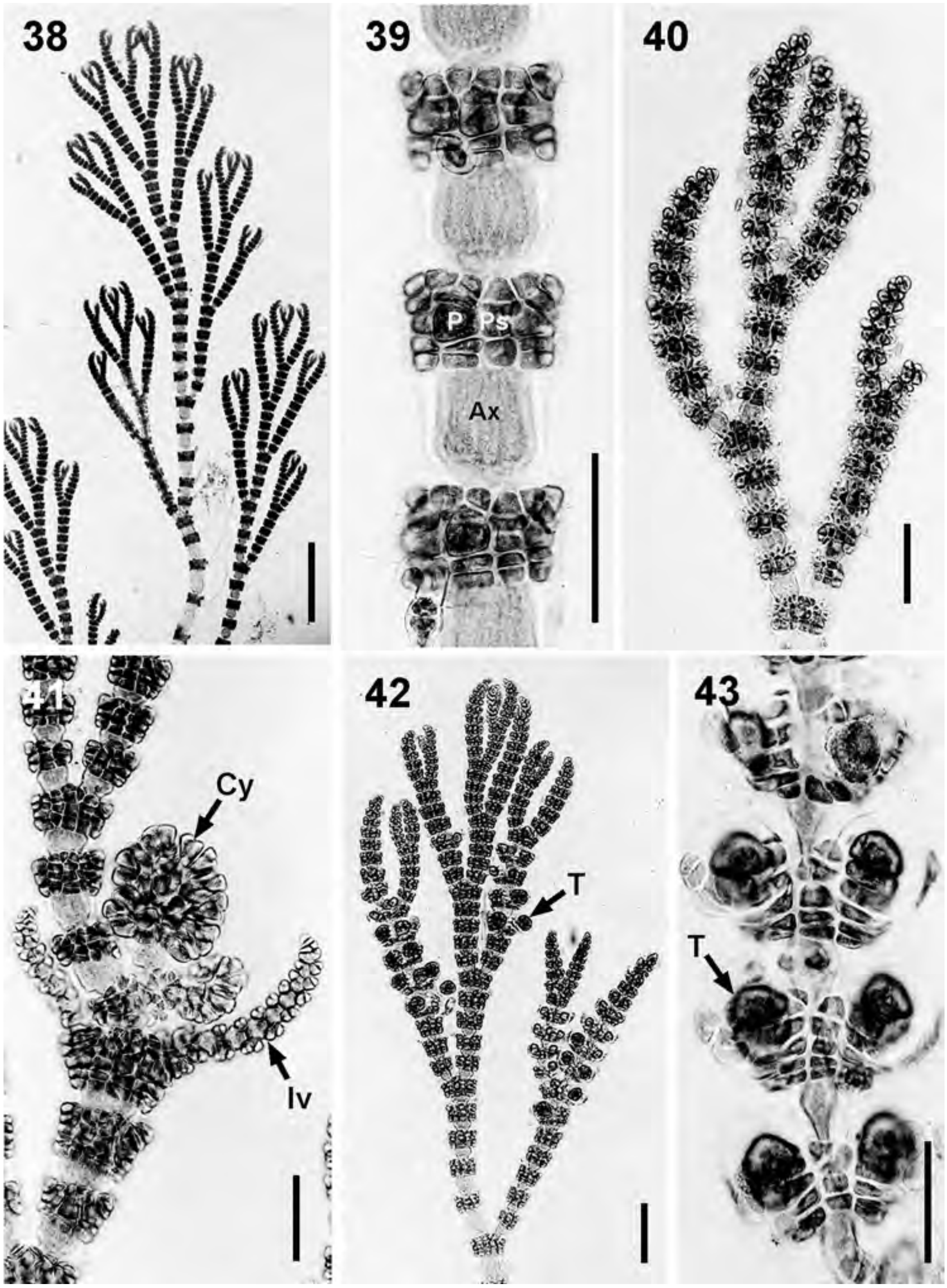
Rhizoids are one-celled and terminate in a digitate pad, or occasionally in unattached, blunt tips (Fig. 5). No more than one rhizoid is produced per periaxial cell.

Reproductive structures. Spermatangia are produced on the adaxial face of a cortical node near the apex (Figs 20, 21, 23) and later around the axis to form a cushion covering the entire cortical surface (Fig. 24). The terminal cortical cells each cut off several spermatangial parent cells, which then elongate and cut off one or two spermatangia terminally by oblique divisions (Fig. 22). Spermatangia are colorless, spherical, 3.8 ± 0.4 µm x 2.7 ± 0.8 µm.

In young female thalli, procarps are produced in a row on the abaxial side near the apex. The carpogonial branches are borne laterally on the supporting cell and are four-celled (Fig. 26). After presumed fertilization, the trichogyne retracts, and the supporting cell enlarges, cutting off the auxiliary cell (Fig. 27). The auxiliary cell then divides into a foot cell and a gonimoblast initial (Fig. 28). The foot cell fuses with the supporting cell and the axial cell, forming a large fusion cell (Fig. 29). The gonimoblast initial then cuts off the first gonimolobe initial terminally followed by one or two additional gonimolobe initials laterally (Fig. 30). Gonimolobe cells are largely transformed into carposporangia at maturity. Mature cystocarps consist of three gonimolobes and are spherical, 116 ± 20 µm x 118 ± 19 µm. They often include two to three gonimolobes and are surrounded by two to four finger-like involucral branches (Figs 25, 31).

Tetrasporangia are distributed in the upper thallus parts (Fig. 32). They are initially produced from the first-formed periaxial cell, next from the last-formed one (Figs 33, 35), and then from the second (Figs 34, 36) and the third (Fig 37), indicating an opposite sequence pattern. Since one tetrasporangium is produced from each periaxial cell (Fig. 37), four tetrasporangia in total make a whorl at each node along the upper axis. Tetrasporangia are fully covered by cortical cells and immersed (Figs 33, 34). They are spherical to ellipsoidal in shape, measure 36 ± 3 µm x 33 ± 2 µm excluding the sheath, and 44 ± 3 µm x 41 ± 2 µm with the sheath. The tetrasporangia appear to be cruciately arranged (Fig. 37).

Photographs of vegetative and reproductive features of *Ceramium recticorticum* are shown in Figs 38-43.



Figs 38-43. *Ceramium recticorticum* Dawson.
Fig. 38. Vegetative thallus. Scale = 200 μm. Fig. 39. Cortical nodes. Scale = 50 μm. Fig. 40. Male thallus. Scale = 100 μm. Fig. 41. Cystocarps (Cy) surrounded by involucral branches (Iv). Scale = 50 μm. Fig. 42. Tetrasporangial thallus with tetrasporangia (T). Scale = 100 μm. Fig. 43. Tetrasporangia along axis. Scale = 50 μm.

DISCUSSION

Our recent collections of *Ceramium recticorticum* agree well in their habit, branching pattern, and arrangement of cortical cells with the original description and illustrations (Dawson, 1950) and with isotype materials. The type [LAM 500108 (AHFH 48795)] is deposited in LAM, but was unavailable for this study. The male and female reproductive structures, which we report here for the first time, conform to those of other published *Ceramium* species (Miranda, 1929; Hommersand, 1963; Boo & Yoon, 1993; Cho *et al.*, 2001a, b).

Ceramium recticorticum is very similar with *C. flaccidum*, *C. fimbriatum*, and *C. gracillimum* var. *byssoideum* (Womersley, 1978; Stegenga & Vroman, 1987) in having horizontally elongate basipetal cell in the cortical nodes and unicellular rhizoids terminating in a pad. However, *C. recticorticum* is distinguished from *C. flaccidum* and *C. fimbriatum* in having only four periaxial cells, and pseudoperiaxial cells in the cortex, and from *C. gracillimum* var. *byssoideum* in having horizontally elongate acropetal cortical cells.

Pseudoperiaxial cells are cut off laterally from periaxial cells in *C. australe* Sonder, *C. macilentum* J. Agardh, *C. shepherdii* Womersley (Womersley, 1978), and *C. clarionense* Setchell et Gardner (Abbott, 1999) as well as *C. recticorticum.* However, the pseudoperiaxial cells of *C. recticorticum* differ from that of *C. australe* in being cut off on the adaxial side of periaxial cell and those of *C. macilentum, C. shepherdii*, and *C. clarionense* in having single acropetal and basipetal cortical cells. The presence and arrangement of pseudoperiaxial cells may be useful in distinguishing some species of *Ceramium*.

Although the corticating initials of *Ceramium recticorticum* are cut off transversally from both the anterior and posterior ends of the periaxial cell, both acropetal and basipetal cortical cells become more horizontally elongated. However, only basipetal cortical cells in *C. gracillimum* var. *byssoideum* or only basipetal corticating initials in *C. fimbriatum* (Nakamura, 1965) and *C. flaccidum* (Womersley, 1978) are horizontally elongated. Our observations appears different from that of Womersley (1978), considering both *C. fimbriatum* and *C. gracillimum* var. *byssoideum* as synonyms of *C. flaccidum*, who described that only a single, elongate derivative is cut off from each periaxial cell and this derivative may then divided in various ways to form a further elongate cell or to cut off two small cells, or the elongate first derivative may divide transversely into 2-4 small isodiametric cells. In other *Ceramium* species except the above four species, the corticating initials are cut off obliquely from each periaxial cell and are spherical to angular in shape (Hommersand, 1963; Womersley, 1978; Cho *et al.*, 2001a, b). Considering that the shape, orientation, and arrangement of the cortical cells in the internodes are diagnostic features for *Centroceras* Kützing and *Corallophila* Weber van Bosse (Norris, 1993; Cho *et al.*, 2000), in which basipetal cortical cells are rectangular and regularly arranged in long vertical rows, features related to horizontally elongated basipetal cells, which are present in *C. fimbriatum*, *C. flaccidum*, and *C. gracillimum* var. *byssoideum*, as well as *C. recticorticum,* may be phylogenetically important.

The rhizoids of *Ceramium recticorticum* are one-celled with a digitate tip. This type of unicellular rhizoid has also been reported in *C. fimbriatum* (Nakamura, 1965; Abbott, 1999) and *C. flaccidum* (Womersley, 1978; Maggs & Hommersand, 1993). However, all other *Ceramium* species have two- to several-celled rhizoids of uniseriate filaments, terminating in multicellular pads (Womersley, 1978; Abbott, 1999; Cho *et al.*, 2001b).

Tetrasporangia offer useful taxonomic characters in many *Ceramium* species (Womersley, 1978). Like those of most incompletely corticated species (Nakamura, 1954; Womersley, 1978), tetrasporangia of *C. recticorticum* are produced from periaxial cells. However, *C. recticorticum* is distinguished by having only one tetrasporangium formed from each periaxial cell. It is clearly different from other incompletely corticated species such as *C. californicum* J. Agardh, *C. cimbricum* H. Petersen *in* Rosenvinge, *C. gardneri* Kylin, *C. paniculatum* Okamura and *C. tenerrimum* (Martens) Okamura, in which two or three tetrasporangia are produced from each periaxial cell (Nakamura, 1954; Cho *et al*., 2001a).

About fifty-seven members of *Ceramium*, including *C. recticorticum*, are recorded from the North Pacific (Setchell & Gardner, 1924, 1930, 1937; Dawson, 1950, 1962; Nakamura, 1965; Itono, 1977; Abbott, 1999). *Ceramium recticorticum* is reported to occur in the Gulf of California from Bahía Bocochibampo near Guaymas, Sonora (type locality), Mazatlan, Sinaloa (Dawson, 1950, 1961, 1962), Balandra and Punta Perico, Baja California Sur, Mexico in this study and from the Galapagos Islands (Dawson, 1963). This limited distribution may indicate its adaptation to the tropical warm waters of the Gulf of California and the Galapagos Islands.

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