Rhizoidal Cortication in the Red Algal Genus *Ceramium* (Ceramiaceae, Ceramiales): Two Developmental Patterns[1]

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Abstract — In studying the morphology and reproductive development in two species of *Ceramium* (Ceramiaceae, Rhodophyta), with emphasis on nodal cortication, two different developmental patterns of rhizoidal corticating cells were found. In *C. personatum* (a species with incomplete cortication), elongate rhizoidal corticating cells are only produced basipetally from periaxial cells at the nodes, whereas in *C. nitens* (a species with complete cortication), they are produced both acropetally and basipetally from periaxial cells and function as inner cortical cells producing the outer cortical cell clusters throughout the thallus. The rhizoidal corticating cells of *C. personatum* typically resemble those of *C. californicum*, while those of *C. nitens* resemble those of *C. boydenii*. The female reproductive structures of *C. personatum*, reported here for the first time, conform to those of other known species of *Ceramium*. Some species, such as *C. nitens*, have rhizoidal corticating filaments and complete cortication, a characteristic of *Campylaephora*; however, these taxa can be distinguished by separated cortication between distal and proximal axial cells of the former *versus Campylaephora*, which has secondary pit-connections between the rhizoidal corticating cells. Our findings support the critical need for a revision of the genera *Ceramium* and *Campylaephora*.

***Ceramium* / Ceramiaceae / eastern Pacific / marine algae / morphology / ontogeny / Rhodophyta / taxonomy / western Atlantic**

Résumé — **Cortication rhizoïdale dans le genre d'algue rouge *Ceramium* (Ceramiaceae, Ceramiales) : deux modes de développement.** Lors de l'étude du développement de la morphologie et de la reproduction chez deux espèces de *Ceramium* (Ceramiaceae, Rhodophyta), étudiant notamment la cortication nodale, deux modes différents de développement des cellules corticantes rhizoïdales, ont été trouvés. Chez *C. personatum*

(espèce à cortication incomplète), les cellules corticantes rhizoïdales allongées sont produites seulement de façon basipète à partir des cellules périaxiales des nœuds ; chez *C. nitens* (espèce à cortication complète), elles sont produites à la fois de façon acropète et basipète à partir des cellules périaxiales et fonctionnent comme les cellules corticales internes qui produisent les massifs de cellules corticales externes dans tout le thalle. Les cellules corticantes rhizoïdales de *C. personatum* ressemblent typiquement à celles de *C. californicum*, tandis que celles de *C. nitens* ressemblent à celles de *C. boydenii*. Les structures femelles de reproduction de *C. personatum* sont décrites ici pour la première fois et sont conformes à celles des autres espèces connues de *Ceramium*. Quelques espèces, comme *C. nitens*, ont des filaments corticants de nature rhizoïdale et une cortication complète, des caractéristiques du genre *Campylaephora* ; cependant, ces taxons peuvent en être distingués par l'existence d'une cortication séparée entre les cellules axiales distales et proximales alors que *Campylaephora* a des synapses secondaires entre les cellules corticantes rhizoïdales. Nos observations confirment la nécessité d'une profonde révision des genres *Ceramium* and *Camplaephora*.

Algues marines / Atlantique occidental / *Ceramium* / Ceramiaceae / morphologie / ontogénie / Pacifique oriental / Rhodophyta / taxinomie /

INTRODUCTION

The genus *Ceramium* Roth (1797: 146) is characterized vegetatively by cylindrical axial cells that are incompletely to completely covered by cortical cells, and by pseudodichotomous branching (Kylin, 1956; Hommersand, 1963; Boo & Lee, 1994; Cho *et al.*, 2002). Although the degree of cortication may depend on the growing season and microhabitat (Garbary *et al.*, 1978; Cormaci & Motta, 1987), the type of cortication pattern is used as a diagnostic character for the taxonomy of the species (e.g., Dawson, 1950; Dixon, 1960; Itono, 1977; Nakamura, 1965; Abbott & Hollenberg, 1976; Womersley, 1978; Cho *et al.*, 2001, 2002, 2003). Some species of *Ceramium*, i.e. *C. personatum* Setchell *et* Gardner (1930: 171), *C. nitens* (C. Agardh) J. Agardh (1851: 130), *C. boydenii* A. *et* E. Gepp *in* E. Gepp (1904: 164) and *C. californicum* J. Agardh (1894: 45), possess elongated rhizoidal corticating cells, while most other species of *Ceramium* bear spherical or ovoid cortical cells. Species of *Ceramium* with rhizoidal corticating cells have usually been transferred to the genus *Campylaephora* J. Agardh (1851: 149; type species: *C. hypnaeoides* J. Agardh), e.g. *C. crassa* (Okamura) Nakamura (1950: 166).

Comparative studies were conducted on the poorly understood Pacific México species, *C. personatum*, based on recently collected specimens from Baja California that included all reproductive stages; and on the western Atlantic *C. nitens*, a common epiphyte reported from Florida to Colombia and the Gulf of Mexico (Taylor, 1960; Ortega *et al.*, 2001), based on liquid-preserved specimens from the Florida Keys and on herbarium specimens from Atlantic Costa Rica. The goal of this study was to elucidate the development of the rhizoidal corticating cells and the developmental patterns in these two species, and further to describe and illustrate the distinct cortication patterns in the tribe Ceramieae (Ceramioideae, Ceramiaceae).

MATERIAL AND METHODS

Collected samples of *Ceramium personatum* from the Pacific Coast of Baja California, México, and *C. nitens* from the Florida Keys, USA, were liquid-preserved in the field in 4% Formalin/seawater. Specimen numbers with the prefix #TOC- refer to the notebooks of Tae Oh Cho. Microscope observations were made from material stained with 1% aqueous aniline blue acidified with dilute HCl (Tsuda & Abbott, 1985). Photomicrographs were taken with a Polaroid DMC Ie digital camera (Polaroid, Inc., Cambridge, MA) attached to an Olympus BX60 microscope and VANOX AHBT3 (Olympus, Melville, NY). Herbarium specimens of *C. personatum* used in this study are deposited in the herbarium of Chungnam National University, Daejon, Korea (CNUK), while material of *C. nitens* is housed in the Algae Laboratory, University of Louisiana at Lafayette (LAF) (herbarium abbreviations follow Holmgren *et al.*, 1990). Images were edited and assembled into plates using *Photoshop* v.5.0 (Adobe Systems Inc., San Jose, CA). A total of 15 individuals were selected from ten tufts in order to access and quantitatively measure relevant characters.

RESULTS

Ceramium personatum Setchell *et* Gardner (Figs 1-9)

Ceramium personatum Setchell *et* Gardner, 1930: 171, pl. 6, figs 1-2; Dawson, 1950: 133; Dawson, Neushul & Wildman, 1960: 11; Dawson, 1962: 62, pl. 29, figs 3-4; Stewart & Stewart, 1984: 145; González-González *et al.*, 1996: 188.

Description: Thalli erect (Fig. 1) and delicate, forming dense tufts, 0.8-1.7 cm high, pseudo-dichotomously to trichotomously branched, rose-red in color, with filiform rhizoids at the base; adhering to paper upon drying. Axes have a forcipulate, slightly curved apical region (Fig. 2); each composed of an axial cell row and corticated nodes; axial cells cylindrical, 217-236 μm(mean = 204 μm) by 73-103 μm (mean = 88 μm) at the seventh order of branching away from the apex.

Cortical development: Five (Figs 5, 6) or 6 periaxial cells are obliquely cut off from the upper part of each axial cell and remain at the nodes after axial cell elongation. The first periaxial cell is cut off on the abaxial side of the third to fourth cell below the apex. The remaining periaxial cells are subsequently cut off in an alternating sequence, first to one and then to the other side of the first periaxial cell. All periaxial cells produce cortical cells that form an incomplete cortex (Fig. 5) covering the axial cells only at the nodes. The cortication consists of the cortical cells and occasional to abundant filiform rhizoidal cells (Figs 3, 4). Four to 5 primary cortical cells (Fig. 5) are produced from each periaxial cell in an alternate sequence, and each cuts off outer cortical surface cells. The first two primary cortical cells are obliquely cut off from the anterior end of periaxial cells and grow acropetally; the remaining two or three are obliquely produced from the posterior end and grow basipetally. The acropetal corticating filaments cut off from the primary cortical cells are 3-4 cells long and predominant (Fig. 4), while the basipetal corticating filaments are 1-2 cells long and present in the lower portion of the thallus. Filiform rhizoidal cells are cut off only basipetally from the periaxial cells (Figs 3, 4) at the nodes in the middle part of the thallus. The rhizoidal cells
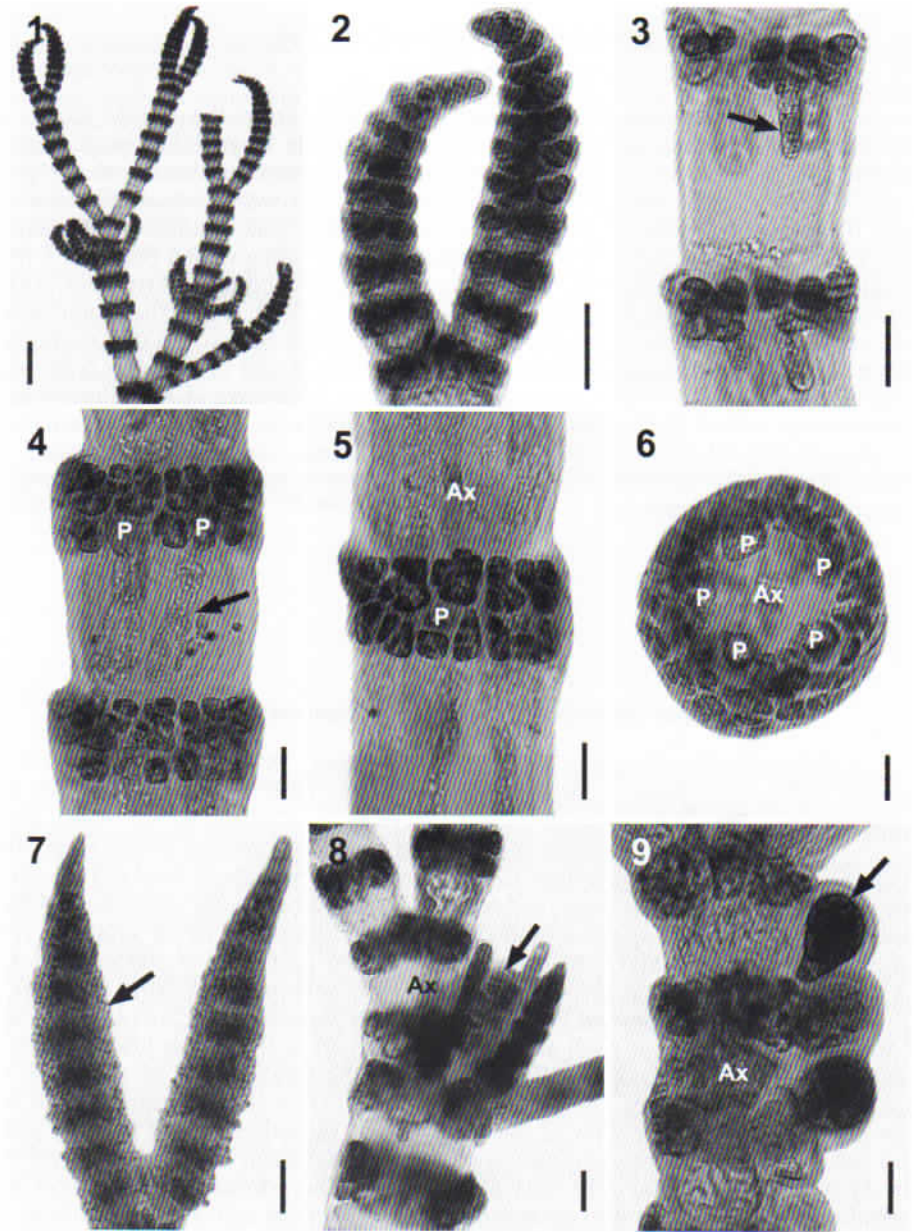
Figs 1-9. *Ceramium personatum* Setchell *et* Gardner from Baja California, Pacific México: Figs 1, 8 (#TOC-004860); Figs 2-6 (#TOC-004864); Fig. 7 (#TOC-004856); & Fig. 9 (#TOC-004860). **1**: Thallus (female gametophyte); scale = 100 μm. **2**: Apical region; scale = 40 μm. **3**: Cortical nodes with young, developing rhizoidal corticating cells (arrow); scale = 20 μm. **4**: Cortical node with mature rhizoidal corticating cells (arrow); scale = 20 μm. **5**: Detail of cortical node lacking rhizoidal cells; scale = 20 μm. **6**: Cross section through cortical node; scale = 20 μm. **7**: Spermatangia (arrow) arranged in whorls; scale = 25 μm. **8**: Young carposporophyte (arrow) surrounded by involucral branches; scale = 20 μm. **9**: Tetrasporangia (arrow) arranged along the axis; scale = 20 μm. (Abbreviations: Ax = axial cell; P = periaxial cell).

elongate (Fig. 4) and occasionally divide, forming up to 3-celled filaments covering the internodal part of the axial cell, and reaching the cortical node below (Fig. 4). Although the cortex is incomplete, the cortical nodes sometimes appear uninterrupted due to the overgrowth of the elongate rhizoidal filaments. No secondary pit connections are established among the rhizoidal and nodal cells.

Male gametophytes: Spermatangia are produced on the adaxial face of a cortical node near the apex and then spread out to form a cushion over the entire cortical surface (Fig. 7). Each terminal cortical cell cuts off several spermatangial parent cells, which then elongate and become rod-shaped, and in turn cut off by oblique division 1 or 2 terminal spermatangia. Spermatia are colorless and subspherical, 3-5 μm (mean=4 μm) by 2-4 (mean = 3μm).

Female gametophytes: An involucre of 3-6 digitate branchlets surrounds the young carposporophyte (Figs 1, 8). Mature cystocarps are spherical, 68-140 μm (mean = 104 μm) long by 73-137 μm (mean = 110 μm) diameter.

Tetrasporophytes: Tetrasporangia are distributed in the upper part of the thallus, first arranged in a single row along the abaxial side (Fig. 9) and then form in 2-4 rows on the abaxial side of each cortical node. Two tetrasporangia develop from each periaxial cell, each slightly covered by cortical cells at the base. They are tetrahedrally divided, spherical to ellipsoidal, and average 51 ± 4 μm by 39 ± 3 μm excluding the sheath, 60 ± 5 μm by 48 ± 4 μm including the sheath.

Habitat: Mid-intertidal to shallow subtidal, up to 10 m depths; growing on hard subtratum, or epiphytic on the seagrass *Zostera marina* L.

Type locality: Isla Guadalupe, off Baja California Norte, México.

Pacific Coast Distribution: Baja California Norte: Isla Guadalupe; Bahía San Hipólito. Baja California Sur: Bahía Magdalena.

Remarks: The known distribution of *C. personatum* was extended to Bahía San Hipólito, Baja California by Dawson *et al.* (1960). Dawson (1962) noted "identity unclear" for specimens from Punta Santa Rosalía (=Rosalillita) and Bahía Ositos, and although reported from Costa Rica (Taylor, 1945, as '*C. personatum*'), Dawson (1950) was of the opinion that those specimens could not be identified with certainty.

Representative specimens studied: *Pacific México- Baja California Sur:* Bahía Magdalena, Puerto 'Lopez Mateos,' Baja California Sur, coll. T.O. Cho & R. Riosmena-Rodriguez, #TOC-004856, #TOC-004857, #TOC-004861, #TOC-004863 (CNUK), #TOC-004858 (CNUK), #TOC-004860 (CNUK), #TOC-004864, #TOC-004859, and #TOC-004905 (vegetative; CNUK), all 29 Nov 1999.

Ceramium nitens (C. Agardh) J. Agardh (Figs 10-20)

Ceramium nitens (C. Agardh) J. Agardh, 1851: 130; Collins & Hervey, 1917: 147; Børgesen, 1918: 244; Taylor, 1960: 535, pl. 16, fig. 14; Soto & Ballantine, 1986: 139; González-González *et al.*, 1996: 103; Ortega *et al.*, 2001: 205.

Basionym: *C. rubrum* η [var.] *nitens* C. Agardh, 1824: 136.

Description: Thalli of erect, completely corticated axes, often slightly secundly branched, with curved apical regions and a sublate apex (Fig. 11); rose-pink in color; forming entangled dense tufts, mostly 10-15 cm high; pseudo-dichotomously to alternately branched in a single plane at irregular interval between branches, with non-forciculate apices (Fig. 10), and filiform rhizoids at the base; adhering to paper upon drying. Axes composed of an axial cell row and corticated nodes and internodes. Axial cells produced by transverse division of the apical cell (Fig. 12); spherical to ovoid, 320-400 μm (mean = 360 μm) by 230-270 μm (mean = 250 μm) at the level of the seventh order of branching away from the apex.
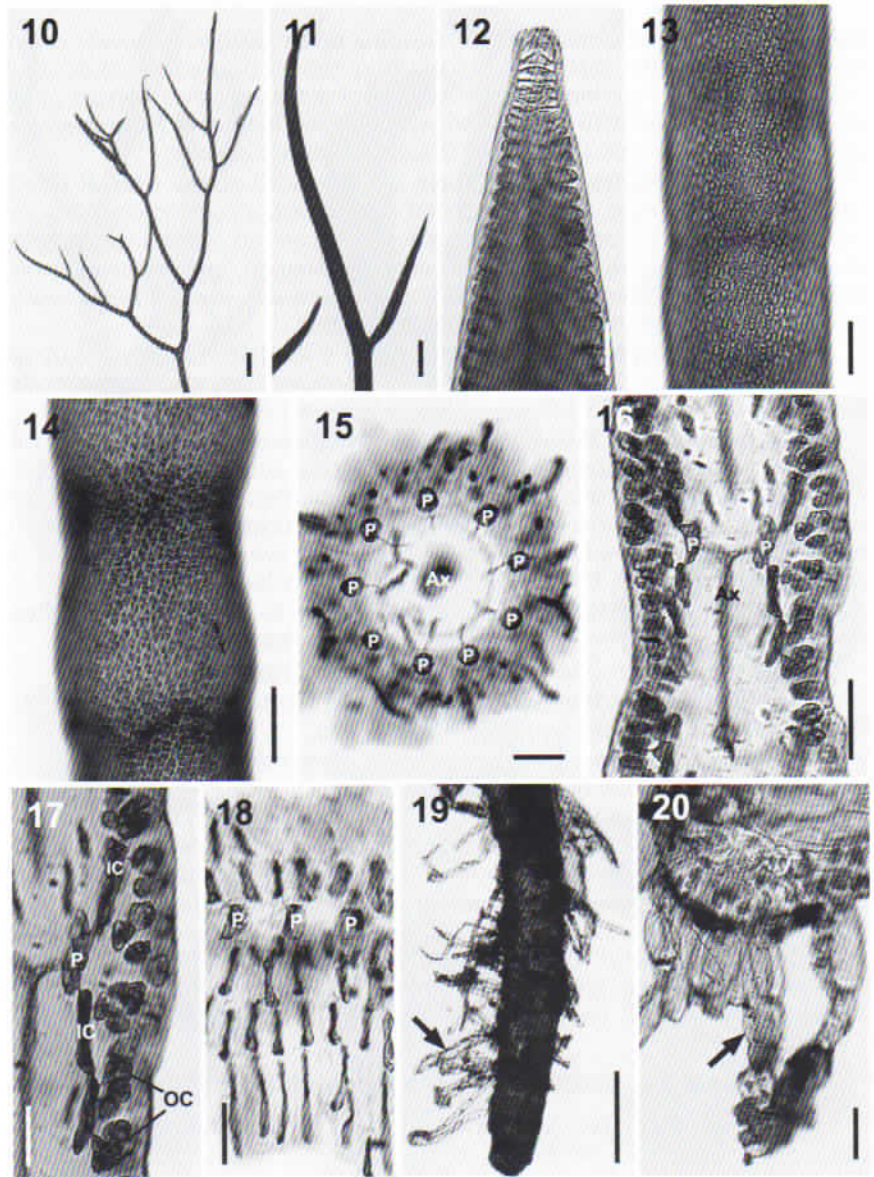
Figs 10-20. *Ceramium nitens* (C. Agardh) J. Agardh from Long Key, Florida, USA (i.e.10-15, & 18: #LAF-12-10-1998); and from Limón, Costa Rica (i.e. 16, 17, 19 & 20: #USJ-A-27768). **10**: Thallus (non-reproductive); scale = 1 mm. **11**: Upper thallus; scale = 0.5 mm. **12**: Apex; scale = 20 µm. **13**: Complete cortication in upper thallus; scale = 50 µm. **14**: Complete cortication in lower thallus; scale = 100 µm. **15**: Transection showing nine periaxial cells; scale = 50 µm. **16**: Longitudinal section showing cortical and periaxial cell arrrangement; scale = 40 µm. **17**: Longitudinal view showing inner cortical and outer cortical cells; scale = 20 µm. **18**: Development of four rhizoidal inner corticating filaments from periaxial cells; scale = 50 µm. **19**: Rhizoids (arrow) at thallus base; scale = 0.5 mm. **20**: Development of rhizoid (arrow) from periaxial and inner corticating cells; scale = 50 µm. (Abbreviations: Ax = axial cell; P = periaxial cell; IC = inner cortical cell; OC = outer cortical cell).

Cortical development: Nine periaxial cells are cut off obliquely from the upper part of each axial cell and remain at the nodes after axial cell elongation (Fig. 15). The periaxial cells are cut off in an alternating sequence on the abaxial side of the fifth to sixth cell behind the apex; each periaxial cell produces corticating filaments that comprise the cortex. Mature cortication is complete throughout the entire thallus (Figs 13, 14), covering the axial cells, and consists of inner filiform rhizoidal cells and small rounded outer cortical cells (Fig. 16). Four primary cortical cells (Fig. 18) are produced from each periaxial cell in an alternate sequence, and continue to grow as rhizoidal inner corticating filaments (Fig. 18); the first two are obliquely cut off from the anterior end of periaxial cells and grow acropetally, while the remaining two are cut off obliquely from the posterior end and grow basipetally. These filiform rhizoidal cortical cells branch pseudo-dichotomously and elongate (Fig. 18), becoming well developed in the middle and lower portions of the frond, but not in the upper portions. The rhizoidal filaments develop into 3 to 6-celled filaments basipetally, and into 2 to 3-celled filaments acropetally (Fig. 18), and cut off outer cortical cell clusters (Fig. 17). The acropetal rhizoidal filaments from one node do not establish secondary pit connections with the basipetal filaments from the upper node (Fig. 16). Outer cortical cells are small, angular and somewhat globular, and organized in clusters of 3 to 4 small surface cells (Fig. 17). Attachment rhizoids produced from periaxial and cortical cells near the base of the thallus are rod-shaped, multicellular, uniseriate, and may terminate in a pad (Figs 19-20). Reproductive structures not observed.

Habitat: Mid-intertidal to shallow subtidal up to 15 m depth; growing on rocks or coral fragments, and epiphytic on, or sometimes entangled with, other green or red macroalgae, or seagrass blades of *Thalassia testudinum* Banks *ex* König or *Syringodium filiforme* Kützing.

Type locality: 'Antillas'(C. Agardh, 1824: 136).

Distribution: Bermuda; Florida to Colombia; southwestern Gulf of Mexico.

Representative specimens studied: *USA* – **Florida**: Monroe County, Long Key, Florida Keys, coll. B. Wysor & T. Francovich, *s.n.*, 10 Oct 1998 (#LAF-12-10-1998; vegetative). *Atlantic Costa Rica* - **Provincia Limón**: Puerto Limón, coll. R. Soto, *s.n.*, 5 Jul 1978 (#USJ-A-22551; vegetative); and, coll. R. Soto, *s.n.*, 21 Oct 1983 (#USJ-A-27768; vegetative); Punta Cahuíta, coll. R. Soto, *s.n.*, 24 Jun 1981 (#USJ-A-22435; vegetative); and Punta Manzanillo, coll. R. Soto, *s.n.*, 30 Sep 1983 (#USJ-A-22688; vegetative).

DISCUSSION

The collections of *Ceramium personatum* studied agree in habit, branching pattern, arrangement of cortical cells, and tetrasporangial development with the original description and illustrations of Setchell & Gardner (1930). The female reproductive structures, reported herein for the first time, conform to those of other species of *Ceramium* (e.g. Miranda, 1929; Hommersand, 1963; Cho *et al.*, 2001, 2002). Setchell & Gardner (1930) and Dawson (1950) commented that *C. personatum* had some similarities with *C. caudatum* Setchell *et* Gardner (1924: 776), and later Dawson (1962) suggested it may prove to be a variant of *C. caudatum*. Dawson (1950) had also suggested it might be related to *C. gardneri* Kylin (1941: 29), and it resembled *C. zacae* Setchell *et* Gardner (1937: 89). However, the

21   **22**   **23**   **24**

Incomplete cortication   **Complete cortication**
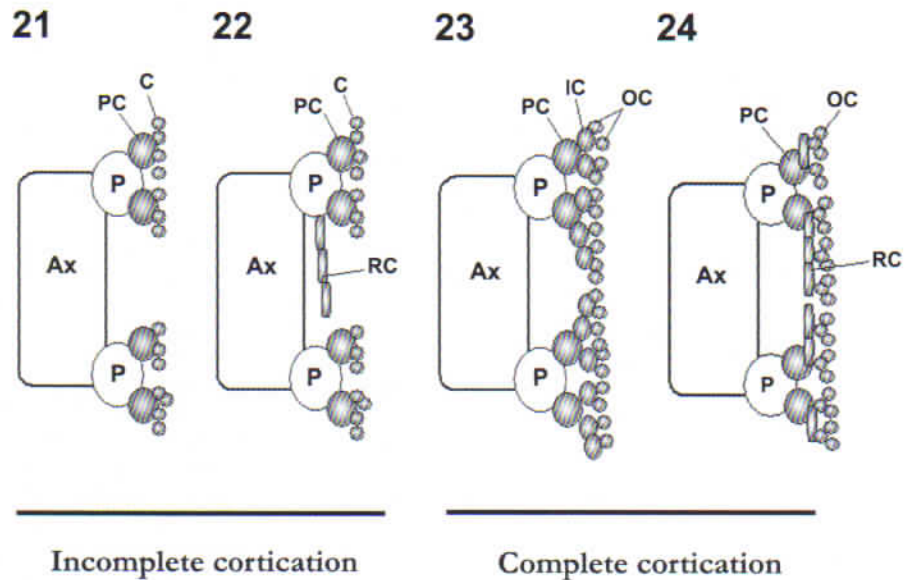
Figs 21-24. Diagrams of incomplete and complete cortication patterns in *Ceramium*. **21**: Incomplete cortication pattern without rhizoidal corticating cells, and each periaxial cell bearing primary and outer cortical cells (e.g., *C. inkuyii*). **22**: Incomplete cortication pattern with rhizoidal corticating cells originating from periaxial cells that also bear primary and outer cortical cells at node (e.g., *C. personatum*). **23**: Complete cortication pattern without rhizoidal corticating cells and with periaxial cell bearing primary, inner and outer cortical cells (e.g., *C. kondoi*). **24**: Complete cortication pattern with rhizoidal corticating cells that are cut off from primary cortical cells that also bear outer cortical cell clusters (e.g., *C. nitens*). (Abbreviations: Ax = axial cell; P = periaxial cell; PC = primary cortical cell; IC = inner cortical cell; OC = outer cortical cell RC = rhizoidal corticating cell).

tetrasporangial arrangement and the presence of rhizoidal corticating cells in all developmental stages indicate that *C. personatum* should be recognized as a distinct species. These rhizoidal corticating cells growing over the internodal cells, are reported in the original description (Setchell & Gardner, 1930), and have been observed in every specimen we studied, and provide a good diagnostic character at the species level (Dawson, 1950).

Our collections of *Ceramium nitens* agree in habit and branching pattern with the descriptions and illustrations of Caribbean specimens (*e.g.* Taylor, 1960). Our observations confirm that *C. nitens* is characterized by an erect thallus with markedly straight segments, a subulate apex, and complete cortication. Previous researchers (e.g. C. Agardh, 1824; J. Agardh, 1894; Taylor, 1960) did not comment on the presence of rhizoidal cortication in the lower thallus of *C nitens*. In our study, we found that the inner rhizoidal corticating cells that bear the outer cortical cells are an important diagnostic character for *C. nitens*.

Cortication pattern is used as a significant diagnostic feature for the taxonomy of *Ceramium* (e.g., Dixon, 1960; Hommersand, 1963; Nakamura, 1965; Itono, 1977; Womersley, 1978; Cho *et al.*, 2002, 2003), with cortication being incomplete (Figs 21, 22) to complete (Figs 23, 24) in varying degrees (Nakamura, 1954;

Womersley, 1978; Maggs & Hommersand, 1993; Cho *et al.*, 2001). Although rhizoidal corticating cells (="rhizoidal filaments in the cortex", see *e.g.* Itono, 1977: 321) are used to characterize the genus *Campylaephora*, they have also been observed in some species of *Ceramium*, including *C. personatum, C. nitens, C. californicum*, and *C. boydenii* (J. Agardh, 1894; Setchell & Gardner 1930; Nakamura, 1954; Cho *et al.*, 2001; herein). Rhizoidal corticating cells are typically elongated and filiform, produced from periaxial or cortical cells (Cho *et al.*, 2001), and can be present in taxa with either incomplete or complete cortication (Figs 22, 24).

In the genus *Ceramium*, two different developmental patterns of rhizoidal corticating cells (Figs 22, 24) can be recognized. The first pattern (Fig. 22) occurs as secondary development in incompletely corticated taxa, and is characterized by having only descending rhizoidal cells within the internodes. These rhizoidal corticating cells may help expand the cortex and protect the axial cell from direct exposure to the environment. Included in this first pattern are two closely related species, *C. personatum* and *C. californicum* (J. Agardh, 1894; Cho *et al.*, 2001). However, the rhizoidal corticating cells of *C. californicum* are produced from both periaxial cells and/or cortical cells (Cho *et al.*, 2001), whereas those of *C. personatum* are produced only from periaxial cells. The other pattern (Fig. 24) occurs in the inner cortical layer of completely corticated species in which rhizoidal corticating cells are cut off from primary cortical cells and, functioning as inner cortical cells, cut off outer cortical cell clusters acropetally and basipetally. This second pattern includes *C. nitens* and the closely related *C. boydenii* (Nakamura, 1954). These elongated inner rhizoidal corticating cells may allow expansion of the cortication by producing several outer corticating clusters. The rhizoidal corticating cells of incompletely corticated species (Fig. 22) are different from those with complete cortication (Fig. 24) in that they grow only basipetally and are less irregular in distribution.

The species of *Ceramium* having rhizoidal corticating cells that form a complete cortex, such as *C. nitens* and *C. boydenii*, are also somewhat similar to the three species of *Campylaephora*. The latter genus has well-developed rhizoidal corticating cells in the inner cortical layer (Dawson, 1950; Nakamura, 1954; Seo *et al.*, 2003). However, *Campylaephora* species also have secondary pit-connections between the rhizoidal corticating cells of the downward formed periaxial cells in the upper axial cell and the upward formed periaxial cells in the lower axial cell. These secondary pit-connections are regarded as one of the diagnostic characters of *Campylaephora* (Nakamura, 1954; Boo, 1985; Seo *et al.*, 2003). Therefore, although the mature cortication of *C. nitens* and *C. boydenii* is similar in appearance to that in *Camplyaephora*, they can be distinguished from the latter in having disjunct cortication (lacking secondary pit connections) between the distal and proximal ends of the axial cell. In conclusion, we recognized that there is critical need for the revision of *Ceramium* and *Campylaeophora*.

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