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Sung Min Boo: Intermediately corticated species, *Ceramium puberulum* (Ceramiaceae, Rhodophyta)

Key Index Words: *Ceramiaceae*—Ceramium puberulum—Mesoceramium—*Rhodophyta*—*Taxonomy*.
Sung Min Boo, Department of Biology, Chungnam National University, Daejon 305–764, Korea

Ceramium Roth is a well-known genus of morphological variability and taxonomic instability in the Rhodophyta. The species occur on most coasts of the world and about 190 species have been credited in the world (Boo and Lee 1993). The taxonomy has been based on vegetative features and tetrasporangial disposition (J. Agardh 1894, Dixon 1960), which have been used in subgeneric grouping as well as description of new taxa. As some diagnostic features were, however, shown to be inconsistent in a species or to be inadequate for a synthetic character, the subgeneric groups proposed by J. Agardh (1894) as well as in the modified scheme (De Toni 1903) have been accepted to be untenable (Hommersand 1963, Womersley 1978). Nakamura (1950) regarded *Ceramium* as a polymorphic genus and separated it into three subgenera; *Hormoceras* with partial cortication, *Mesoceramium* with intermediate cortication and *Euceramium* with full cortication. He gave no satisfactory explanations on *Mesoceramium*, that is probably due to the absence of the members in his material. Although many studies have been carried out on either the *Hormoceras* or the *Euceramium* species in the field as well as in culture (see Boo and Lee 1993), there are few reports on the detailed structure and reproduction of the *Mesoceramium* species.

Ceramium puberulum was originally described by Sonder (1845) from Western Australia. It occurs from Dongarra, West Australia, to Wilson's Promontory, Victoria and northern Tasmania (Womersley 1978, p. 217). The plants are usually epiphytic on seagrasses, *Posidonia* and *Amphibolis* species. The species is characterized by the intermediate cortication in main axis and primary to secondary spines on the whole plant. In addition to the description by Womersley (1978), the present paper gives further observations on the structure and reproduction of *C. puberulum* and discusses the taxonomic significance.

During July 1987, material for observation was collected on Aldinga beach, South Australia. Some 81 specimens, all of which were epiphytic on *Posidonia sinuosa* Cambridge et Kuo, were collected, comprising 45 cystocarp-bearing female, 16 male, 9 tetrasporic and 11 sterile plants (Boo, July 1987: Herbarium of the Department of Biology, Chungnam National University, Daejon, 001027). For microscopic examination, materials were stained with 0.5% aniline blue and acidified with about 1% hydrochloric acid. Herbarium specimens were also available: the Agardh herbarium, LD; the Thuret herbarium, PC; AD. Herbarium abbreviations are according to Holmgren *et al.* (1990).

Observations: Plants (Fig. 1A) are 5–10 cm long and light to dark red in color. They are attached by rhizoids to *Posidonia* and are erect and much branched. Rhizoids are produced from periaxial, inner and outer cortical cells. They aggregate and form a compact discoid holdfast. Plants are pseudodichotomously branched and 25 to 30 lateral branches are produced on a main axis.

Main axis consists of axial, periaxial and cortical cells. Axial cells are produced from the oblique division of apical cells. The diameter including cortical cells ranges from 162 to 440 μm with a mean of 269 ± 63 μm and the length from 162 to 580 μm with a mean of 376 ± 87 μm ($n = 55$) in the middle between the 8th and the 11th dichotomy from apex. Seven to eight periaxial cells are alternately formed from each axial cell (Fig. 4B).

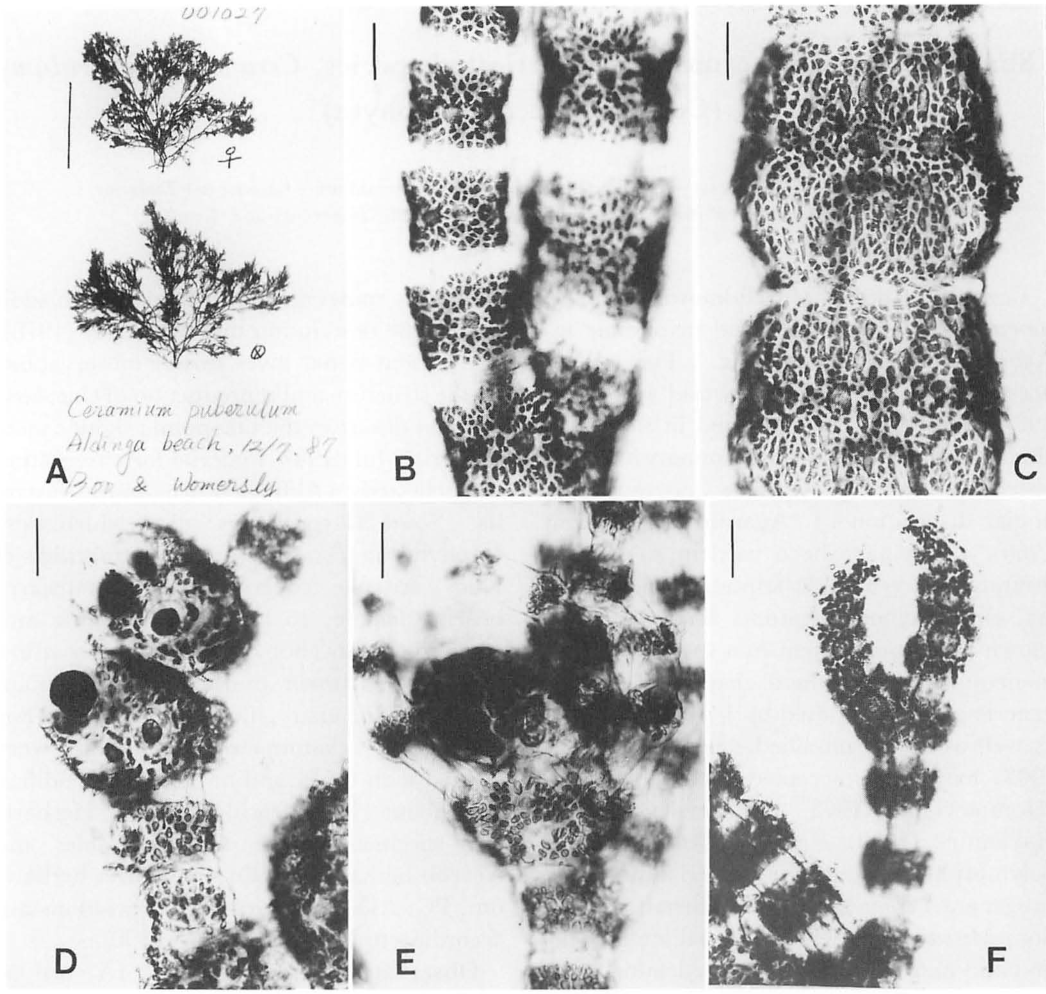

Fig. 1. *Ceramium puberulum* (Herbarium of the Department of Biology, Chungnam National University, 001027). A: habit of a cystocarp-bearing female and a tetrasporic plant (Scale bar 2 cm). B: Partly corticated node. C: fully corticated node. D: Tetrasporangial branch. E: Cystocarp and involucral branches. F: Spermatangial branch (Scale bars 100 μm).

Cortical cells are produced in basipetal and acropetal directions from the periaxial cells (Fig. 2A-D). Inner cortical filaments are well developed from periaxial cells in the lower axis, and are elongate, slender and branched dichotomously. Cortical cells envelope only the nodes in upper branches while inner and outer cortical cells entirely cover the lower whole axis (Fig. 1B-C). The ratio of the length of the cortical band to the length of the axial cell, which is taken from the middle node in each dichotomy, shows that the axes from apex to the thirteenth or fourteenth dichotomy are incompletely corticated while completely corticated below it (Fig. 3).

Spines are produced from periaxial cells in upper branches (Fig. 4A). They are one to several in a node and up to five-celled. In the lower axis, small spines are produced from cortical cells and are one- to two-celled.

Branches are formed at irregular intervals of 3-5 nodes. Branching pattern is pseudodichotomous to alternate. Adventitious branches are frequently produced from periaxial cells. They are short and occur at very irregular intervals.

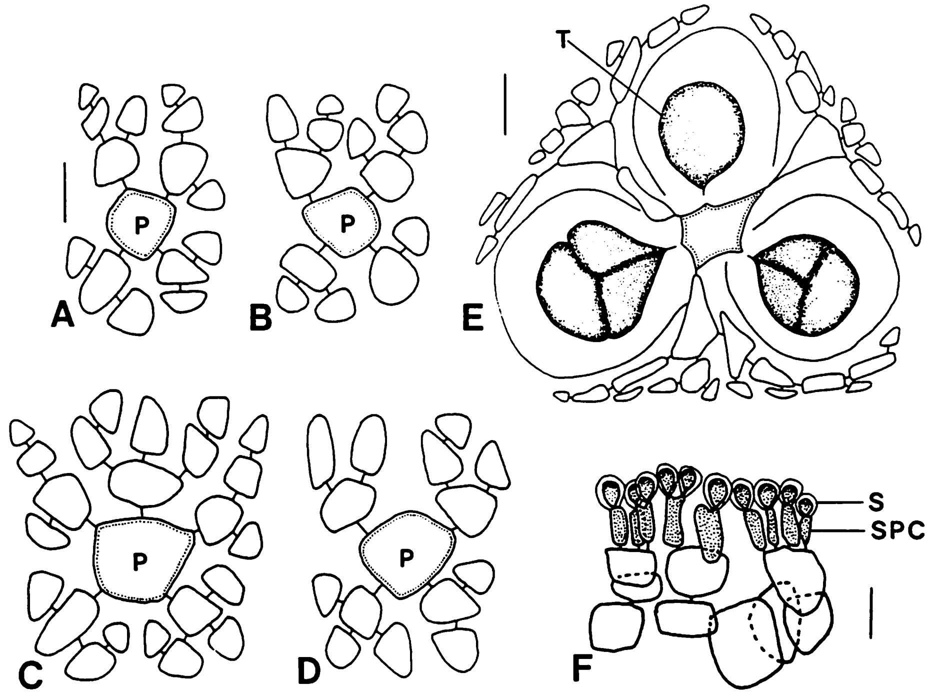

Fig. 2. *Ceramium puberulum*. A–D: Development of cortical cells from a periaxial cell (Scale bars 50 μm). E: Formation of three tetrasporangia from a tetrasporangial mother cell (Scale bar 50 μm). F: Spermatangial formation (Scale bar 80 μm) (P: periaxial cell, S: spermatangium, SPC: spermatangial parent cell, T: tetrasporangium)

Tetrasporangia are usually produced from the middle to upper region of main branches, but rarely occur on the lower fully corticated axis. They are at first single but later several per node, and are normally in unilateral and abaxial rows (Fig. 1D). The first-formed periaxial cell produces several cortical cells and becomes a tetrasporangial mother cell. One to three tetrasporangia are formed from a single periaxial cell (Fig. 2E) and form a rounded tetrasporangial group. All tetrasporangia are entirely enveloped by small cortical cells and become prominent on nodes, with no naked regions between the nodes. The tetrasporangia measure 95±11 μm×82±7 μm (n=33) including sheath and 71±13 μm×62±9 μm excluding sheath. The division is tetrahedral.

Carpogonial branches are usually produced in the abaxial side of the upper region of main branches (Fig. 4A). A vegetative cell group is at first produced from the first-formed periaxial cells (Fig. 4B) and consists of two to several cells. It stops growth after fertilization and remains attached even until the formation of gonimolobes. Carpogonium

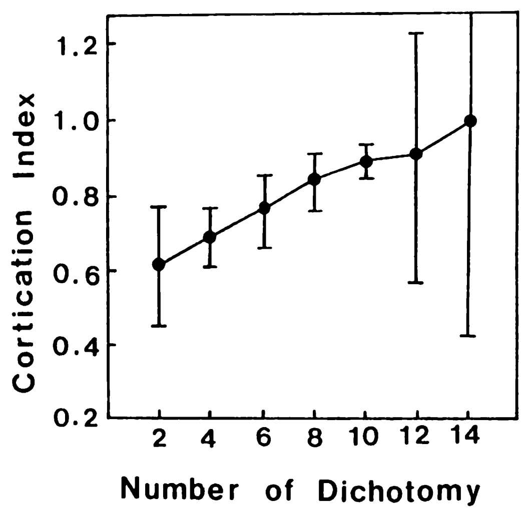

Fig. 3. Cortication index in the middle node of each dichotomy in plants (n=21) with about twenty-seven dichotomous branches (mean±SD). Below the 14th dichotomy, main axes are completely corticated.

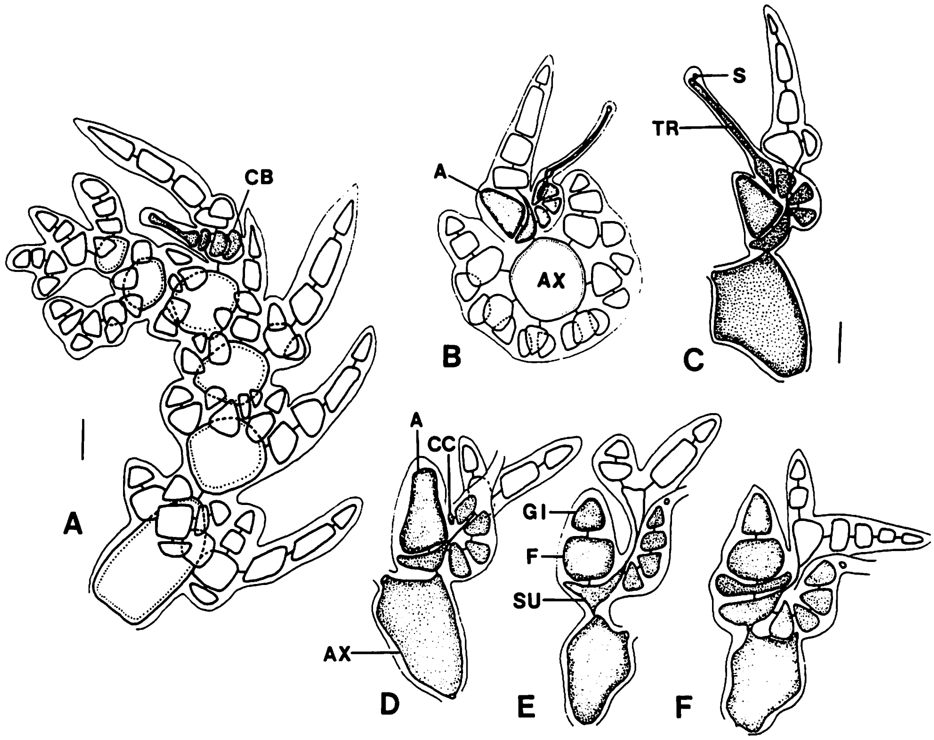

Fig. 4. *Ceramium puberulum.* A: Young branch with a carpogonial branch (Scale bar 50 μm). B: Cross section of cortical node with a carpogonial branch. C: A spermatium attached on trichogyne. D: A connecting cell cut off from carpogonium. E: Formation of a foot cell and a gonimoblast initial. F: The first division of a gonimoblast initial (Scale bars 60 μm). (A: auxiliary cell, AX: axial cell, CB: carpogonial branch, CC: connecting cell, F: foot cell, GI: gonimoblast initial, P: periaxial cell, S: spermatium, SU: supporting cell, TR: trichogyne)

always originates from the same first-formed periaxial cells and carpogonial branch is four-celled with a long slender trichogyne (Fig. 4B). When a spermatium is attached on the thichogyne apex and fertilization is completed, the supporting cell produces an upper auxiliary cell (Fig. 4C). The carpogonium synchronously produces a small connecting cell toward the auxiliary cell (Fig. 4D) and this connecting cell fuses with the auxiliary cell. The auxiliary cell divides into an upper gonimoblast initial and a lower foot cell (Fig. 4E). In later stages, axial cell fuses with the supporting and the foot cell and the fusion cell mechanically supports gonimoblasts. The gonimoblast initial (Fig. 4F) produces two to three gonimolobe initials which divide to become gonimolobes of a spherical carposporophyte (Fig. 1E), measuring 250±42 μm × 232±44 μm (n=37). They are surrounded by (5)-6-(7) involucral branchlets, which are produced from the periaxial cells below the axial cell bearing gonimolobes.

Spermatangia are produced from the middle to the upper region of main branches, which are partly corticated at the nodes, while absent on the growing apex or on the fully corticated lower axis. They initially occur on the adaxial side of branches and later cover the whole cortical nodes, forming dense patches (Fig. 1F). All cortical cells at upper branches can lose plastids and become spermatangial parent cells. Each spermatangial parent cell produces one to two spermatangia as clavate protrusions (Fig. 2F). Spermatangia are colorless, elliptical to spherical and measure 2-4 μm × 3-6 μm.

Discussion: Rhizoidal morphology has been known as a diagnostic character for separating *Ceramium* from the related genus, *Campylaephora*. According to Nakamura (1950, 1954, 1965), filamentous rhizoids occur in the former genus while discoid ones occur in the latter genus. *Ceramium puberulum* has a compact discoid holdfast, that may imply the relationship to *Campylaephora* species. It is probable that the discoid holdfast is developed as a result of an epiphytism on seagrasses and other hard plants, that requires reappraisal on the diagnosis of *Campylaephora*.

The pattern of cortical development is one of the most important characters in the genus *Ceramium* and the taxonomic importance has fully been discussed by Dixon (1960) and Womersley (1978), with detailed observations on many species. Recent culture studies, however, have shown the plasticity in cortication degree in different culture conditions (Cormaci and Motta 1987, Garbary *et al.* 1978). *C. puberulum* typically shows partial cortication on upper branches while elongate and slender inner cortical cells are well developed on lower axis and, with small and round cortical cells, entirely cover it. The cortication index also implies that the cortication is gradually developed from the upper portion to the lower portion of thallus, as seen in Figure 2. Many specimens are deposited in the Agardh herbarium (LD 20728-85), LD, the Thuret herbarium (numbers not given), PC and AD (A43888 and others), from within the geographic range from Western Australia to Tasmania. The herbarium material shows the same habit and cortical morphology as the plants from Aldinga beach. The intermediate form of cortication is considered to be a consistent and good character for *C. puberulum*, but culture studies would be valuable.

There are two types of spines in the genus *Ceramium*; the primary spines from periaxial cells and the adventitious ones from cortical cells (Dixon 1960). Although only one type of spines occurs in most species, primary spines in *C. puberulum* are three- to five-celled on young branches while the adventitious ones are one-celled on older axes. In this point, it is related to *C. flabelligerum* J. Agardh, but the latter species is distinguished by being fully corticated.

Tetrasporangial division and disposition should be assessed with caution for the diagnostic value and taxonomic utility in *Ceramium* species. Tetrasporangia of *C. puberulum* divide tetrahedrally and are unilaterally arranged. Tetrasporangia in *Ceramium* show a consistent form of division (Hommersand 1963, Boo 1985), but often divide tetrahedrally to cruciately in a single species (Rosenvinge 1924, Dixon 1960, Womersley 1978). Furthermore, in two Australian species, opposite to unilateral tetrasporangia are found in the different portions of main branches (Womersley 1978).

As is seen in Figure 2C, two to three tetrasporangia in *C. puberulum* originate at a same time from a single periaxial cell (Fig. 2C) and form a rounded tetrasporangial group. This is the same with the figure (as *Celeceras monilis* Kützing) of Kützing (1862, pl. 95b, d), according to Womersley (1978), which must have been mis-interpreted as galls by Dixon (1960, p. 347). Since the previous reports on the genus show that a single tetrasporangium originates from a single periaxial or a cortical cell (Dixon 1960, Hommersand 1963), the taxonomic value of tetrasporangial formation in *C. puberulum* needs further comparative studies with other taxa.

The sexual reproductive organs agree well with the previous descriptions on other *Ceramium* species (Miranda 1929, Hommersand 1963, Itono 1977, Gillis and Coppejans 1982, Boo and Lee 1985). Although two carpogonial branches are reported to occur on a basal cell (Janczewski 1876, Rosenvinge 1924, Dammann 1930, Dixon 1960), a single carpogonial branch is found on a basal cell in *C. puberulum*, as is the case of most species of the genus. The fertilized carpogonium is connected with the auxiliary cell by a small connecting cell; this agrees well with *C. flabelligerum* (Miranda 1929) but not with American species which have connecting filaments (Hommersand 1963). There is also a report that supporting cell functions directly as the auxiliary cell (Nakamura 1954). The spermatangial features show no differences with those of other *Ceramium* species (e.g. Hommersand 1963).

As indicated in the introduction, Nakamura (1950) established the subgenus *Mesoceramium*, which was typified with *Ceramium fruticulosum* Kützing. He argued that the primitive cortication type in *Hormoceras* [as in *C. codii* (Richards) G. Mazoyer] progressed through an intermediate type in *Mesoceramium* to the ultimate development in *Euceramium*, that seems to give a phylogenetic relationship to the cortication degree. The subgenera were adopted in his later publications (Nakamura 1954, 1965) and by Itono (1981), but *Hormoceras* and *Euceramium* were already not recognised by Womersley (1978). There have, however, been no comments on the included taxa and circumscription of *Mesoceramium*.

Ceramium fruticulosum, which occurs on the European coast, is distinguished by the intermediate cortication, the absence of spines and two carpogonial branches on a single supporting cell (Rosenvinge 1924, Boo unpublished). There are no detailed studies on the nodal cortication in the field, but it depended on the culture conditions (Garbary *et al.* 1978). According to Feldmann-Mazoyer (1940), *C. flabelligerum* var. *mediterraneum* Debray from Europe has the intermediate cortication and spines, that shows the close relationship to *C. puberulum*. Because of insufficient materials of Debray, she didn't reach any conclusion. I tried to find Debray's herbarium, but without success. *C. puberulum* also belongs to *Mesoceramium* on the basis of intermediate cortication, but other vegetative and reproductive features accord with the general description of *Ceramium*. Except for these three taxa, there are few other species with the intermediate cortication in the genus. The present information on *Ceramium* is too insufficient to conclude which feature is more significant in evolution and phylogeny. There are also no discussions on the phyletic relationships in the *Ceramium* species. The above facts show that the establishment of the subgenus *Mesoceramium*, which should be circumscribed by the cortication degree only, is unreasonable.

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S. M. Boo：部分的に皮層を持つ種，*Ceramium puberulum*（イギス科，紅藻）について

部分的に皮層をもつ種である *Ceramium puberulum* Sonder の形態及び生殖について，南オーストラリアアルデインガ海岸より採取した材料と Agardh ハーバリウム，Thuret ハーバリウムからの標本をもとに，詳細に比較・観察した。その結果，単一の四分胞子母細胞から 1－3 ケの四分胞子嚢が形成されるのを除くと，他の栄養細胞及び生殖細胞の特徴は *Ceramium* 属にみられるものとよく一致した。最近，皮層化の程度の *Ceramium* 属における系統進化上の重要性については否定的な見解がなされていることも考慮すると，皮層化の程度で設立された亜属 *Mesoceramium* の存続はあまり意味のないものと思われる。(Department of Biology, Chungnam National University, Daejon 305-764, Korea)

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