

Anatomical characteristics of *Laurencia papillosa* (Rhodomelaceae, Rhodophyta) from Guam and Palau

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Abstract—Some morphological characters of the red alga *Laurencia papillosa* (C. Agardh) Greville are clarified, based on an examination of the type specimen and materials from Guam and Palau. All axial segments of the sterile branchlet have two pericentral cells. In the stichidium, however, one additional pericentral cell is produced per axial cell. The second and the additional pericentral cells always become the fertile pericentral cells to produce a tetrasporangium at distal ends, whereas the first pericentral cell always remains sterile. Epidermal cells do not elongate radially or form a palisade layer in transverse section of branchlets.

Introduction

Laurencia papillosa was first introduced by Forsskål (1775) as *Fucus papillosus* and Turner (1808) later described it as *Fucus thyrsoides*. However, C. Agardh (1822) transferred it to *Chondria* as *C. papillosa*, recognizing that Turner's epithet was a later homonym of *F. papillosus* Gmelin (1768). Then Greville (1830) placed it in the genus *Laurencia*. Despite its long history, however, this taxon has remained very poorly understood. The lack of knowledge of this species has resulted in some synonyms or homonyms and made it one of the most troublesome species in the genus. This study presents anatomical details of sterile and tetrasporangial plants of *L. papillosa* and clarifies some morphological characters based on the examination of the type specimen of the species.

Materials and Methods

Materials of *L. papillosa* (RT 2595, II-9-69 and RT 4135, I-13-71, leg. R. T. Tsuda) from Guam and Palau, respectively, were used for the present study. The type specimen (Holotype: Herb. Forsskål. No. 886) preserved in the Botanical Museum, University of Copenhagen, Denmark was also examined. The sectioning and observation methods for microscopic examination are the same as those given in Nam & Saito (1990).

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Observations

GENERAL EXTERNAL FEATURES

Thalli are 5 to 10 cm high, terete or locally slightly angular to subcompressed, cartilaginous, very rigid and adhere to paper poorly or not at all. One or more erect axes arise from a discoid holdfast and are very densely clothed, except in the lower parts, with numerous truncate, wart-like ultimate branchlets measuring 0.3–0.5 mm in diameter. Branching is more or less patent, irregularly alternate from all sides, subopposite or subverticillate. All branches are slightly attenuate at the tip. Tetrasporangial branchlets are cylindrical and somewhat elongated, and are occasionally branched, giving a compound aspect.

VEGETATIVE STRUCTURES

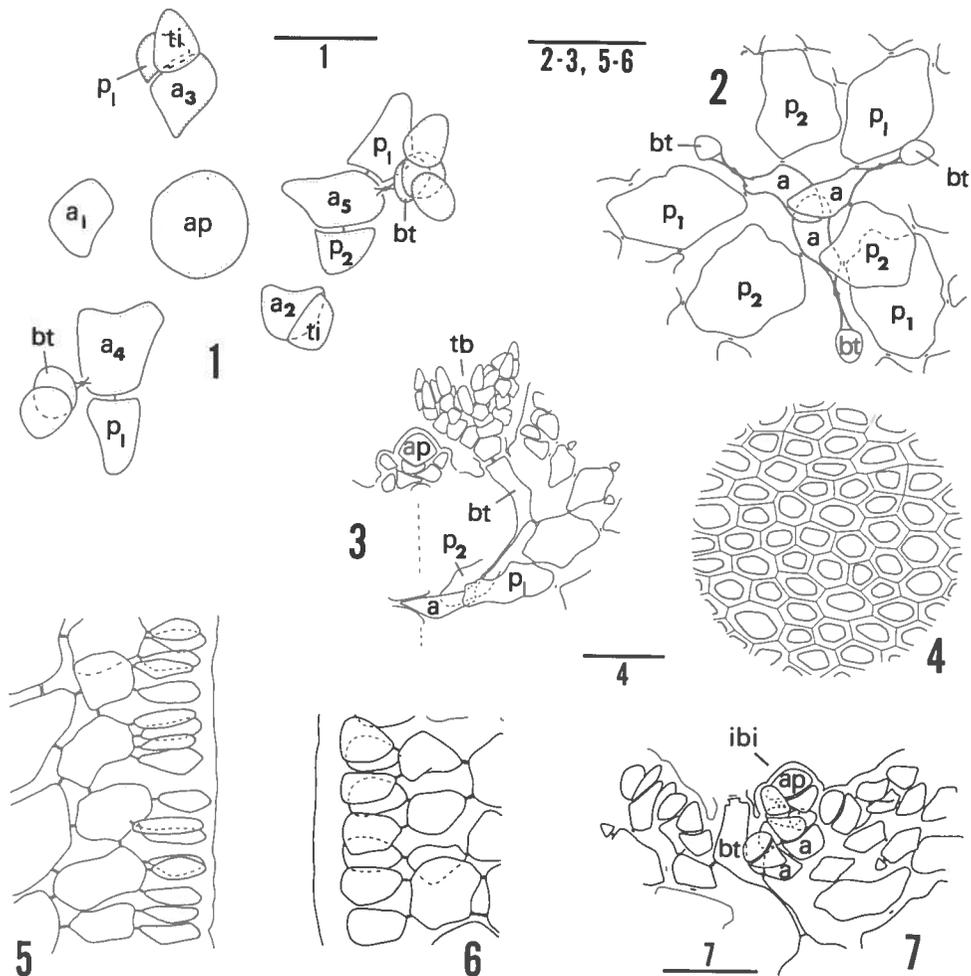
The apical cell, which is always sunk in the depression of branchlet apex, cuts off axial segments successively at its posterior end (Figs 1, 3). The wedge-shaped axial segments, due to oblique divisions, are arranged along a $3/8$ spiral, clockwise or counterclockwise as seen from the apex, since they continue to divide with three dividing faces. Each of the axial segments forms a trichoblast and two pericentral cells (Figs 1, 2).

At first, the initial of the trichoblast is obliquely cut off at the upper side of the axial cell which lies adjacent to the second segment from the apical cell. Then, the two pericentral cells are alternately produced. The first pericentral cell is cut off laterally at the right or left of the trichoblast initial, and then the second at the opposite side of the first. The first pericentral cell is always in position a shorter distance from the trichoblast initial as compared with the second (Figs 1, 2). Their positions are invariable in a given branch system. The positional relationship between the two pericentral cells is determined by the spiral direction of the axial segments. In the branch system with counterclockwise spiral, the first is always produced at the left of the trichoblast initial in all axial segments.

The pericentral cells produce two to four derivatives, each of which divides several or more times in the same manner to give rise to the filaments of determinate growth. The filaments develop quickly in a radial direction with some distortion, and are compacted (i.e., pseudoparenchymatous), while each cell except the terminal cells is connected by secondary pit connections with adjacent cells of filaments which are derived from the same and successive axial segment. The inner condensed structure forms the cylindrical thallus. The basic structure of the thallus, however, is recognizable only in the limited region very close to the apex of the branchlet, because of the thick cortication formed by the abrupt enlargement of the axial segments and their derivatives, and the distortion of the filaments.

The development of trichoblasts is the same as that described in *L. cartilaginea* Yamada (Nam & Saito 1990).

Ordinary indeterminate branches are borne in the axils of the basal cells of the trichoblasts in the apical depression (Fig. 7). They are successively produced with somewhat regular or irregular, short intervals, and most of them develop



Figures 1-7. *Laurencia papillosa*. Figure 1. Serial axial segments segregated in optical transverse section of branchlet apex, showing the sequence of the formation of a trichoblast and two pericentral cells. (Scale bar: 15 μm). Figure 2. Transverse section at some levels near the apex of branchlet, showing three axial segments each of which is provided with a basal cell of trichoblast and two pericentral cells. Figure 3. Young trichoblast and axial cell with two pericentral cells in median longitudinal section through the apex of branchlet. Figure 4. Epidermal cells in surface view of branchlet. Figure 5. Epidermal cells in longitudinal section of branchlet. Note their elongation. Figure 6. Transverse section of branchlet, showing the epidermal cells. (Scale bar: 60 μm for Figures 2-6). Figure 7. Stage in the initiation of indeterminate branch in the axil of the basal cell of trichoblast, as seen in longitudinal section of branchlet. (Scale bar: 30 μm .)

Abbreviations used in Figures 1-10: a, axial cells; ap, apical cell; bt, basal cell of trichoblast; fp, fertile pericentral cell; ibi, indeterminate branch initial; p, pericentral cell; po, postsporangial cover cell; pr, presporangial cover cell; stk, stalk cell; t, tetrasporangium initial; tb, trichoblast; te, tetrasporangium; ti, trichoblast initial. (The numbers 1, 2, etc., indicate the sequence in the formation of the axial and the pericentral cells).

into the short branchlets. The thallus becomes densely clothed with numerous ultimate branchlets (Figs 12–14). In these newly produced branches, the sequence of the development of the basic structure is similar to that described above. The spiral direction of the daughter axial segments, however, seems to be opposite to that of the parent branch. It appears that the two counter spiraling systems occur alternately in the daughter and parent branches.

Adventitious branchlets growing indeterminately are not distinguishable because the ordinary lateral branches usually remain as short branchlets.

The secondary cortex formed by rhizoidal filaments rarely develops in the branches, except near the holdfast.

Epidermal cells are not projected near the apex of branchlets. They are neither elongated radially nor arranged like palisade cells in transverse section of the branchlet (Fig. 6), but are remarkably elongated in longitudinal section (Figs 5, 18). Secondary pit connections are never observed between the epidermal cells (Figs 4, 5).

Lenticular thickenings are absent in the walls of medullary cells. Thickened walls, however, are common in medullary cells.

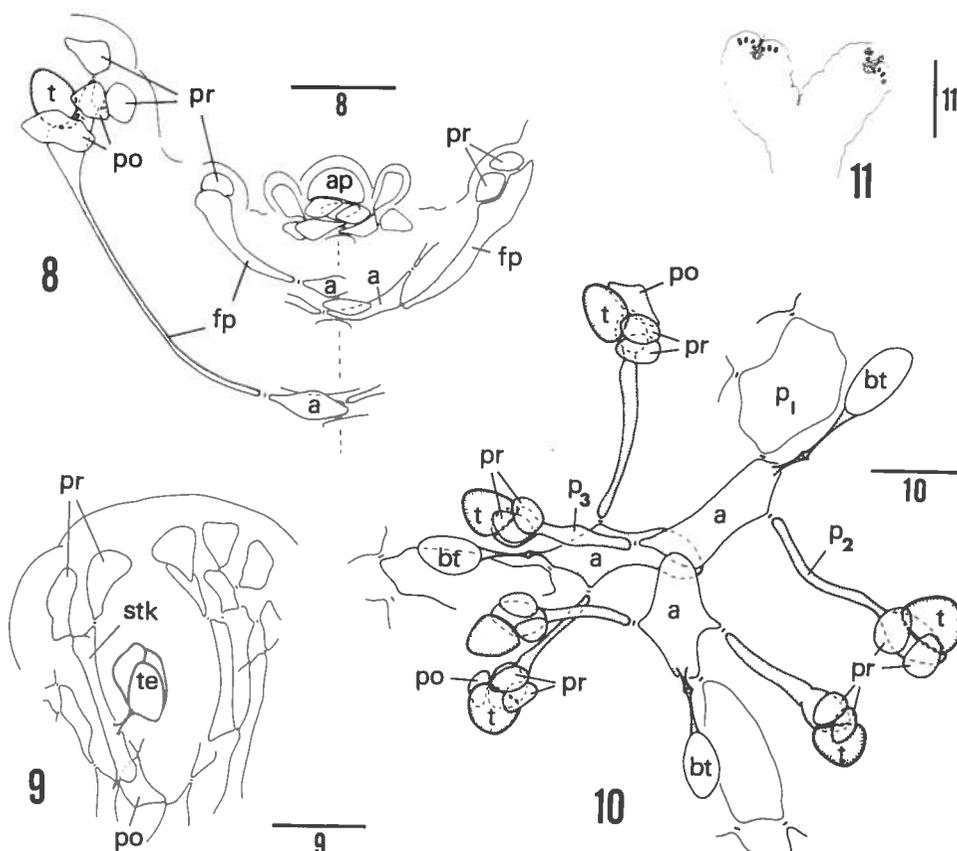
“Corps en cerise” are not detected in the materials preserved in formalin seawater.

DEVELOPMENT OF THE TETRASPORANGIA

Tetrasporangia are borne on the pericentral cells near the apical cell sunk in the apical depression of branchlets (Figs 8, 10). The fertile pericentral cell first cuts off two cover cells (presporangial cover cells) successively at its upper side, and then the tetrasporangium initial is produced abaxially by a concave septum. Next, the residual stalk cell cuts off the third cover cell (postsporangial cover cell) at its side, to the right or to the left. The two presporangial cover cells remain undivided, forming the pair of large cells between which, presumably, the tetraspores escape when mature, whereas the postsporangial cover cell continues to divide, producing the corticating system around the developing tetrasporangium (Figs 8–10). The former is basically arranged at right angles to the direction of the central axis in the surface view of the stichidium and does not form secondary pit connections with adjacent epidermal cells, as in *L. cartilaginea* Yamada (Nam & Saito 1990).

The tetrasporangium initiated near the apical cell is gradually displaced toward the outer side of the apical depression. The stalk cell is drawn out into a long and narrow cell caused by its displacement of the tetrasporangium, since the central axis of the stichidium continues to grow (Fig. 8). Eventually, the elongated stalk cell is separated from the axial cell and the tetrasporangia, which are divided tetrahedrally during the displacement, are scattered near the periphery of the apical depression (Figs 9, 11). The mature tetrasporangia are about 70–100 μm in diameter.

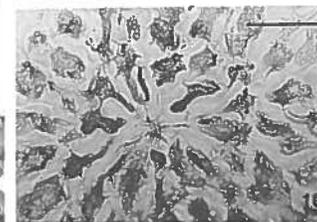
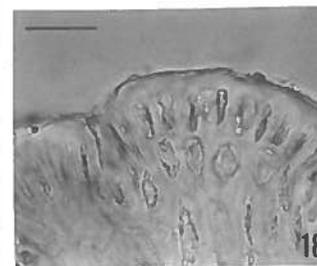
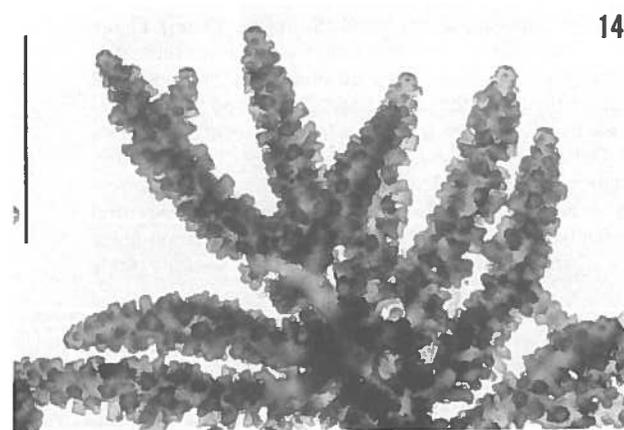
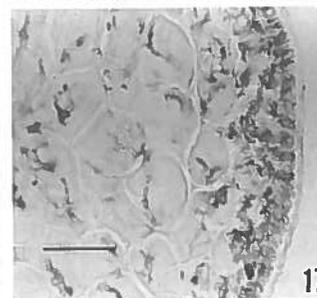
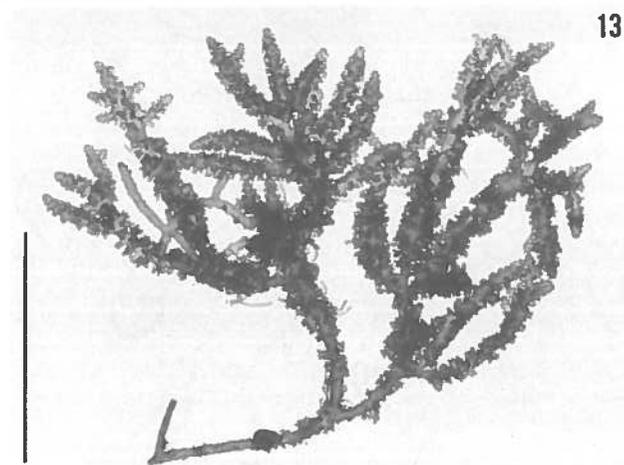
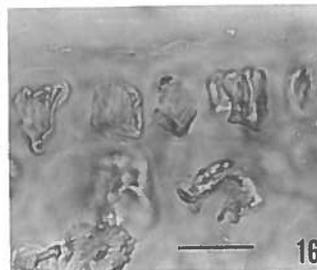
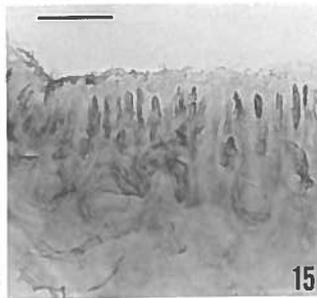
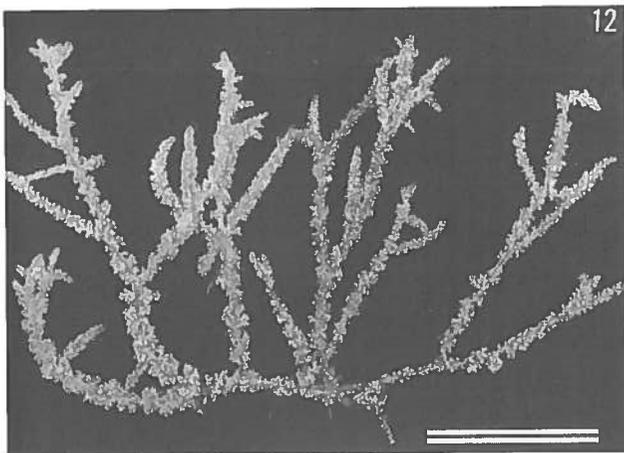
Each axial segment of the stichidium usually bears two fertile pericentral cells, of which one is homologous to the second pericentral cell of vegetative branches, and the other is the third pericentral cell produced only in the stichidium (Fig. 10). The first pericentral cell of the axial segment is always sterile.



Figures 8–11. *Laurencia papillosa*. Figure 8. Development of tetrasporangium and its cover cells seen in median longitudinal section through the apex of stichidium. Note the division of postsporangial cover cell. (Scale bar: 30 μ m). Figure 9. Longitudinal section of stichidium, showing somewhat mature tetrasporangium, its two presporangial cover cells remained undivided, stalk cell and branched postsporangial cover cell. At about this stage, the postsporangial cover cell and its derivatives are usually undistinguishable from adjacent cells. (Scale bar: 60 μ m). Figure 10. Optical transverse section near the apex of stichidium, showing three axial segments each of which is provided with two fertile pericentral cells including an additional fertile one. Note the second pericentral cell developing into fertile one. (Scale bar: 20 μ m). Figure 11. Tetrasporangia scattered near the apex of stichidium as seen in longitudinal section. (Scale bar: 1 mm).

Discussion

Yamada (1931) described and illustrated *Laurencia papillosa* after examining the type specimen preserved in Forsskål's herbarium. His illustrations, however, are not sufficient to adequately circumscribe this species. Moreover, some of his comments are in error. For instance, "The surface cells are very strongly elongated radially in the cross-section of branchlets and arranged like palisade cells." Ac-



According to the present observation of the type specimen (Herb. Forsskål. No. 886 [Copenhagen]: the same specimen examined by Yamada), the surface cells were never elongated radially (Figs 16, 17) but were elongated longitudinally (Fig. 15), and a palisade layer of the surface cells was not clear in the cross section (Fig. 16). The palisade structure is not always evident and so is not useful as a criterion. Another species about which there is confusion is *L. capituliformis* Yamada, which was placed under section Cartilagineae Yamada by Yamada (1931) himself and which later was transferred under Yamada's agreement (personal communication) to section Palisadae Yamada by Saito (1967). Surface cells of many species tend to be more elongate in longitudinal section rather than in transverse section of branchlets, according to our observations.

As seen in this species, fertility of the second pericentral cell in the stichidium was observed only in members of section Palisadae (Nam 1990). Although not examined in the present species, the formation of four pericentral cells in the fertile segment of the female trichoblast is also found only in members of that section (Nam 1990). Accordingly, the importance of the character proposed by Yamada seems to diminish in characterizing section Palisadae.

On the other hand, there are some specimens with four such pericentral cells which are also densely clothed with numerous ultimate branchlets as in *L. papillosa*. They include specimens from Australia and the Philippines that have been identified as *L. papillosa*. They are, however, quite different from *L. papillosa* in anatomical features, such as number of pericentral cells of the axial segment, position of fertile pericentral cell in stichidium and presence or absence of additional fertile pericentral cell (Nam 1990). *L. papillosa* sensu Cribb (1958) from Queensland may also prove to be different from *L. papillosa* in the anatomical features. *L. papillosa* sensu Kang (1966) from Korea is different from *L. papillosa*. *L. papillosa* as reported by Okamura (1902, 1916) in Japan also appears to be a doubtful record. On the other hand, Ganzon-Fortes (1982) described *L. tranoi* as a new species from the Philippines but the specific characters appear to be within the boundaries of *L. papillosa*.

Acknowledgements

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Figures 12–19. *Laurencia papillosa*. Figure 12. Tetrasporic plant in dried specimen from Palau (Jan. 13, 1971, RT 4135). (Scale bar: 2 cm). Figure 13. Tetrasporic plant preserved in formalin-seawater from the same locality. (Scale bar: 3 cm). Figure 14. Part of the tetrasporic plant. (Scale bar: 1 cm). Figure 15. Longitudinal section of ultimate branchlet of holotype specimen (Herb. Forsskål. No. 886), showing the elongated epidermal cells. Figures 16 & 17. Transverse section of ultimate branchlet of the holotype specimen showing the cuboidal epidermal cells. (Scale bar: 25 μ m for Figure 16; 100 μ m for Figure 17). Figure 18. Epidermal cells in transverse section of ultimate branchlet of the present materials from Palau. Figure 19. Axial cell row in transverse section of branchlet of the present materials from the same locality. (Scale bar: 50 μ m for Figures 15, 18 & 19).

to Dr. Jøgen Benth Hansen of Botanical Museum, University of Copenhagen for loan of the holotype specimen of *L. papillosa*.

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