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YOSHIKAWAI OKAMURA (CERAMIACEAE, RHODOPHYTA)  
AND ITS SYSTEMATIC POSITION

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# VEGETATIVE STRUCTURES OF *PLUMARIELLA* *YOSHIKAWAI* OKAMURA (CERAMIACEAE, RHODOPHYTA) AND ITS SYSTEMATIC POSITION

By

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## Abstract

Vegetative structures of *Plumariella yoshikawai* OKAMURA (Ceramiaceae, Rhodophyta) are described and compared with some other related representatives of Ceramiaceae. The axial cortications of this species are initiated by the branchlets produced on the basal segments of the lateral branches and these branchlets divide progressively upwards, laterally, and even downwards. *Plumariella yoshikawai* is recognized as morphologically similar to those of *Balliella* ITONO et TANAKA and *Delesseriopsis* OKAMURA in several features, and in particular, in the pattern of axial cortication, branching pattern and in having cruciate tetrasporangia produced on the segments of branchlets. These branchlets occur on the basal segments of branchlets which originate from the basal segments of lateral branches. These features indicate that *Plumariella yoshikawai* should be placed under the tribe Delesseriopsieae.

It is suggested that, in the evolution of the Ptiloteae from the Antithamnieae, the members of the tribe Delesseriopsieae might have been the link between these two tribes.

## Introduction

The genus *Plumariella* was established and assigned under the Ptiloteae by Okamura (1930:24) based on the features of axial cortications and on the presence of the cruciate tetrasporangia. *Plumariella* is monotypic, and the only representative of the genus is *Plumariella yoshikawai* which has been recorded from the restricted areas of Japan, i.e., Pacific coast of central Japan and the Seto Inland Sea. Kylin (1956) described the genus as having cortical layers which are directed only in an upward direction and as having cruciate tetrasporangia. Although the generic assignment of the genus under the tribe Ptiloteae have been made (Okamura, 1936; Kylin, 1956), details of the vegetative developments and reproduction of the species have remained relatively poorly known.

Recently Itono & Tanaka (1973) carefully studied the members of the tribe Delesseriopsieae, which is thought to be closely related to members of Antithamnieae,

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and their observations show that *Plumariella* is closely related to the Delesseriopsieae.

The present paper reports the results of morphological observations in *Plumariella yoshikawai* and discusses the relationship of this species with other members of the Ceramiaceae.

### Materials and Methods

Specimens used for detailed morphological investigations, which are now in the herbarium of the Department of Biology, Faculty of Science, Kagoshima University, were collected by Dr. M. Yoshizaki of Toho University on the central Pacific coasts of Japan at Kurosaki, Kanagawa Prefecture (April 7, 1967). The materials (*no HI 19795*) are tetrasporophytic and possess many tetrasporangia.

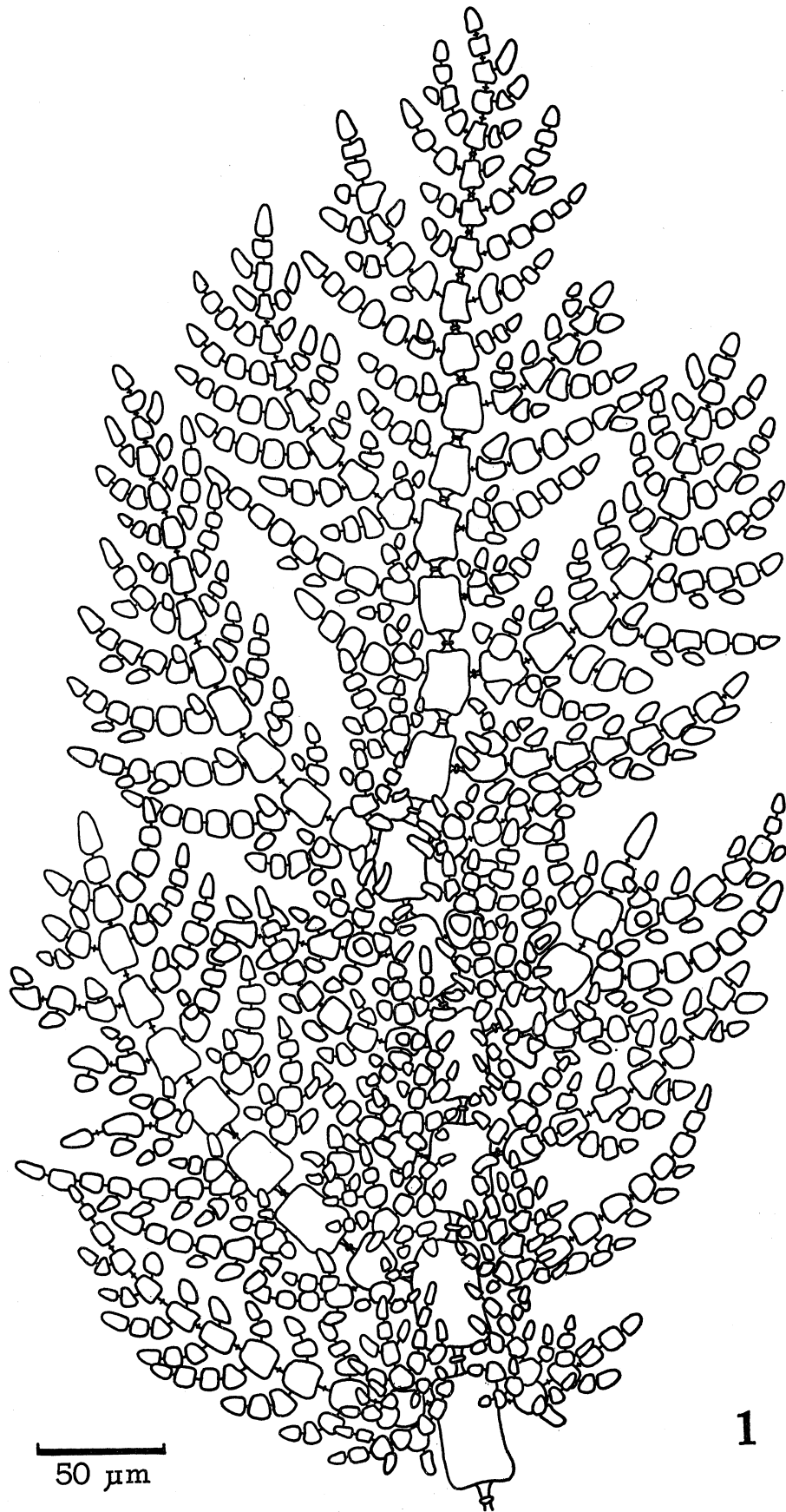
Materials for microscopic study were fixed in 4 per cent formaldehyde in seawater, stained in 1 per cent aqueous methylene blue, acidified, and finally mounted in 80 per cent corn syrup preserved with phenol.

### Observations

The thallus is uniaxial and the growth is initiated by an apical cell that divides transversely into two cells of approximately the same size. The segmental cells enlarge soon after they are produced, and the fully mature axial cells are cylindrical measuring 3–4 times as long as broad. Each of the axial segments has a pair of opposite lateral branches. The initial of a lateral branch originates near the apex (usually three to four segments below the apex) as a protrusion from one side of an axial cell that is later cut off. Two such initials are produced in a regular sequence in each segment and the second initial is opposite the first. The initiation of the first initial in a segment is precisely determined in relation to the segment below. The divergence of the first-formed lateral branches usually generates in a longitudinal pair and the second-formed lateral branches generate in an opposite longitudinal pair to the first ones. The initiation of the first-formed lateral branches in the longitudinal pair alternates to the right and to the left at every two axial segments in the main axis. In figure 1, the first-formed lateral branches in the longitudinal pair in the basal and in the suprabasal segments are produced on the left side of the axis; in the basal third and fourth axial segments they are produced on the right side of the axis and in the basal fifth and the sixth axial segments they are oriented on the left side of the axis. On the other hand, the second-formed lateral branches in the longitudinal pair in the basal and the suprabasal segments are oriented to the right side of the axis, in the basal third and the fourth segments they are on the left side, and in the basal fifth and the sixth segments they are on the right side of the axis. This sequence in the initiations of the first- and second-formed lateral branches in the indeterminate axes is regularly maintained

Fig. 1. *Plumariella yoshikawai* OKAMURA

Apex, showing the origins of lateral branches and the cortical branchlets, and the arrangements of first- and second-formed lateral branches.



throughout the thalli. Diagrammatic representation of the branching pattern in *Plumariella yoshikawai* is presented in figure 2, showing the arrangements of the first-formed and the second-formed lateral branches.

Generally, the first-formed lateral branches are longer and more vigorously branched than those of the second-formed ones which remain short and underdeveloped. The upper branches in the longitudinal pairs, regardless to the first- or second-formed branches, are generally more developed than those of the lower ones.

The fundamental branching manner of *Plumariella yoshikawai* is generally identical with those of *Balliella subcostatum* (ITONO) ITONO et TANAKA of the tribe Delesseriopsieae (Itono & Tanaka, 1973) and of *Plumaria elegans* of Ptiloteae (Kylin, 1956).

At first, the basal cells of the lateral branches are attached to the middle of the axial cell. The part of the axial cell below the pit connection later extends to a length three to four times as great as its diameter. In older segments, the basal cells of the lateral branches are consequently attached at the distal end of the parent axial cell (Fig. 7).

Each segment of the lateral branches, except the basal ones, is provided with the distichous branchlets on the abaxial and the adaxial sides. The branches of all orders are directed towards the apices of the axes, and the abaxial branchlets are generally longer than those of the adaxial side (Figs. 1, 5).

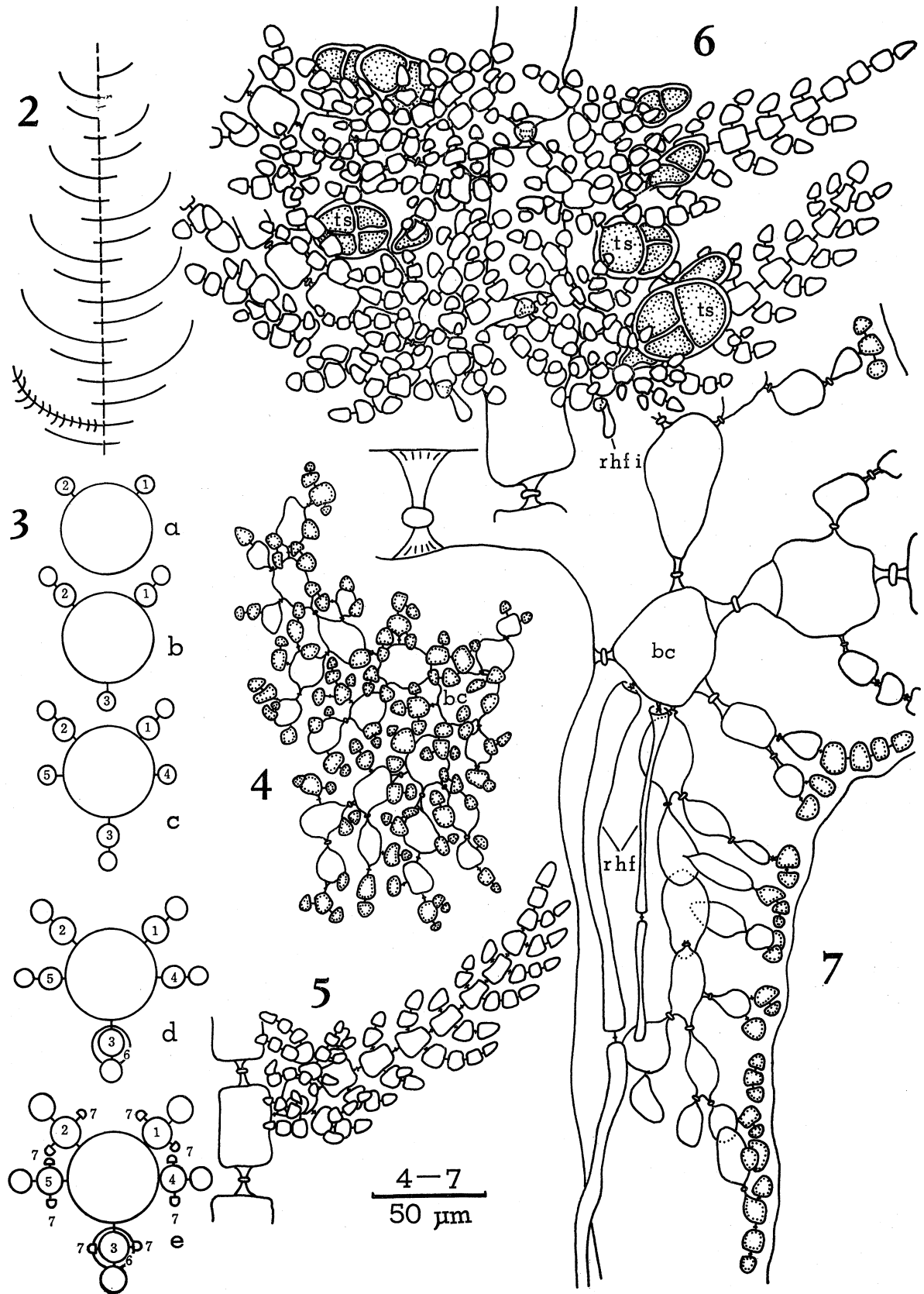
The basal axial segments of branches and branchlets are capable of producing several clusters of branchlets which constitute the cortical layers of an axis in subsequent stages.

In the basal segments of the lateral branches and branchlets of the vigorously growing axes, each segment first produces a pair of branchlets (Fig. 3a, 1-2) on the upper shoulders of the segmental cells, and these branchlets develop progressively than those produced in the subsequent stages. The third branchlets (Fig. 3b, 3) is produced from the abaxial distal end of the segment and the branchlet is directed towards the apex of the lateral branch. The fourth and the fifth branchlet-initials (Fig. 3c, 4-5) are produced on both laterals of the axial segment in opposite pair. The sixth (Fig. 3d, 6) is produced from the abaxial, proximal side of the axial segment and is directed

Figs. 2-7. *Plumariella yoshikawai* OKAMURA

Fig. 2. Diagram of the pattern of branching. Fig. 3. Diagrams to show initiation of branchlets (1-6) on the proximal segments of lateral branches. These branchlets (1-6) produce pseudoparenchymatous cortex around the axes in subsequent stages. Fig. 4. Divisions of branchlet, produced laterally on the basal segment of lateral branch on the right side of the indeterminate axis, showing the directions of divisions. Fig. 5. Determinate branch showing arrangement of lateral branchlets. Fig. 6. Part of indeterminate axis showing axial cortications, arrangements of tetrasporangia (ts) and the initiation of descending rhizoidal filaments (rhfi). Fig. 7. Optical longitudinal section of indeterminate axis.

bc: basal cell of lateral branches or branchlets; rhf: rhizoidal filament; rhfi: rhizoidal filament initial; ts: tetrasporangium; 1, 2, ... 6: indicate the sequence in the formation of the branchlets on the proximal segment of lateral branch.



downwards. These initials of branchlets branch by a process of budding. First an initial cell divides transversely into two nearly equal cells. The lower cell then bulges from its distal end and produces one or two additional apical cells which lie at the same level as the first. All series of segments in the filaments comprising branchlets that originate from the same cell grow to the same length, and the branching of branchlets, therefore, has fundamentally the appearance of being trichotomous or dichotomous. The proximal cells of these branchlets thus produced frequently initiate 2-4 additional initials of branchlets (Fig. 3e, 7). However, the productions of these initials of branchlets (Fig. 3a-e, 1-7) are the typical example, and in some proximal segments of the lateral branches some initials of these branchlets are frequently aborted. The initials of these branchlets (Fig. 3a-e, 1-7) divide progressively so as to envelope the axes of the indeterminate branches and of the determinate lateral branches. In weakly developed determinate branches, only the proximal segment of the branches is provided with the branchlets that corticate the axes. The branchlets divide more progressively towards the indeterminate axes than to the lateral margins of the axes. Figure 4 shows the branching directions of the branchlet which is formed laterally on the proximal segment of the right side branch. The basal segment of the lateral branches are at first almost the same size as in other axial segments, but in the lower fully corticated parts of the thalli they are smaller than those of the other axial segments of the laterals.

The indeterminate axes of *Plumariella yohikawai* are corticated throughout the thalli, except for the terminal more or less younger parts of the axes. The axial cortications are initiated by the productions of the descending rhizoids (Figs. 6-7, **rhf**) and by the productions of branchlets on the proximal cells of the laterals. The descending rhizoidal filaments (Fig. 6, **rhfi**) which corticate the axis arise from each proximal cell of the lateral branches or of the branchlets produced on the proximal cells of lateral branches, beginning at a time when the axial cortications by the branchlets on the proximal cells of the lateral branches are initiated well behind the apex (Fig. 7, **rhf**). Few rhizoid initials (1-3) are cut off from the lower side of the segments, and each rhizoidal filament grows downwards over the axial cells. The rhizoidal filaments are unbranched and they loosely intertwine and clothe the axial segments loosely in the older parts. The cells of the rhizoidal filaments are narrow measuring about 20  $\mu\text{m}$  broad and 10-13 times as long as broad. Another manner of axial cortication formation depends, as mentioned above, on the progressive divisions of the branchlets produced on the basal segments of the laterals. These branchlets are directed on all sides of the axes (Fig. 4), some are ascending or directed transversely, and others are directed downwards. This manner of cortication is not known among members of the tribe Ptiloteae. Okamura (1930) described the cortications of *Plumariella yohikawai*, in which the cortications of the axes are initiated by only ascending branchlets. This feature, as observed by Okamura, is seen only in the younger parts of the thalli; however I did not see such cortication in the lower parts of the thalli.

In fully corticated parts of the thalli, the cortical layers are two or three cell layers thick, and the cells of the inner one or two layers are large and more or less ovate, producing an outer layer of almost spherical, small cells (Figs. 4, 7). The cells of the outermost cells are deep stainable with methylene blue and the cortex is continuous throughout the thalli except for the younger parts of the axes (Figs. 1, 6).

In *Plumariella yoshikawai*, it is difficult to differentiate between indeterminate branches and determinate branches in the younger parts of the thalli, but it is easy to distinguish them in the middle to lower parts of the thalli. From the precise observations on the sequences of the arrangements of first- and second-formed branches and the indeterminate laterals on the axes, it becomes evident that the branches of unlimited growth replace some of the upper branches of the first-formed longitudinal pairs of lateral branches. These branches destined to be of unlimited growth are originally provided with laterals on the abaxial and adaxial sides of the axes as in other determinate branches, in which the laterals are initiated irregularly (Fig. 5). Later, they provide the laterals in the regular manner as in the primary indeterminate branches which branching manner has been described before (see p. 40). The initiations of the laterals in regular sequences in the branches of indeterminate growth occur at the axial segments well above the proximal segments, and, thus, these indeterminate branches are provided with the laterals of irregular sequences in the lower segments and with the laterals of regular sequence in the middle to upper parts of the axes (Fig. 2). Production and the arrangement of the indeterminate branches in the axes occur at irregular intervals of the axial segments. No indeterminate branches of different origin, other than described above, was found in the materials used in the present observations.

Gland cells are totally absent.

Tetrasporangia (Fig. 6, **ts**) are produced singly or in groups of two on the inner segments of the branchlets that are produced on the basal segments of both determinate and indeterminate branches. The segments which form tetrasporangia are usually restricted to the basal and suprabasal axial segments of the branchlets, but, rarely, some tetrasporangia appear to be produced terminally of the branchlets.

A tetrasporangium is initiated as a protrusion from the distal end of a segment. It is usually sessile and does not replace a branch. As many as two tetrasporangia may be produced on the same segment and the latter formed tetrasporangium is smaller than the first tetrasporangium. The contents of the tetrasporangium divide cruciately, and the mature tetrasporangia are globose in shape measuring  $26-30 \times 34-39 \mu\text{m}$  in diameter. The wall that surround the mature tetrasporangium is apparently one layered.

No gametophytic plants was observed in the present study.

### Discussion

*Plumariella yoshikawai* is morphologically distinct and is characterized by a combination of the following features based on the results obtained in the present



observations and in references to the previously made publications (Okamura, 1930, 1936).

- (i) Growth in length takes place by an apical cell that divides transversely into two cells of approximately the same size.
- (ii) The initial of the lateral branch protrudes from one side of an axial cell and the initial is cut off by longitudinal division, and initiates a lateral branch before the opposite lateral branch is formed.
- (iii) The first-formed lateral branches and the opposite second-formed ones in longitudinal pairs are beset in an alternate distichous manner at every two axial segments.
- (iv) Indeterminate branch replaces some of the upper branches in the first-formed longitudinal pairs.
- (v) The proximal segments of the lateral branches of all orders are capable of producing branchlets that corticate the axes of indeterminate growth.
- (vi) The major axial cortications are initiated by the divisions of the branchlets which are produced on the proximal segments of the lateral branches. The branchlets are directed not only towards the upper parts but also in transverse or downwards directions, and the branchlets generally divide more progressively towards the directions of the axes of unlimited growth.
- (vii) The contents of the tetrasporangium are divided cruciately. The tetrasporangia are usually produced on the basal or suprabasal segments of the branchlets which are produced from the proximal cells of the laterals.
- (viii) Carposporophytes are sessile and produced laterally on the branches. Mature carposporophytes are surrounded with many involucre (Okamura, 1930). In reference to the Okamura's illustration, mature carposporophyte is situated well behind the apex. This suggests that maturation of the carposporophyte does not stunt the growth of indeterminate axes.

Although the genus *Plumariella* has been placed under the tribe Ptiloteae, no appropriate features that place the genus under Ptiloteae has been given (Okamura, 1936; Kylin, 1956). *Plumariella* is monotypic and the type of the genus is *P. yoshikawai* known from the restricted areas of Japan. The genus has been distinguished from other members of Ptiloteae by having cruciate tetrasporangia and by the presence of cortical layers initiated upwardly directed branchlets (Okamura, 1930). Although the robust habit and the presence of corticated indeterminate axes relate *Plumariella yoshikawai* to the tribe Ptiloteae, the features used by Okamura (1930) and those made in the present observations suggest *Plumariella yoshikawai* to be erroneously placed under the tribe Ptiloteae.

The Delesseriopsieae (Itono & Tanaka, 1973; including *Balliella* and *Delesseriopsis*) do show several features in common with *Plumariella yoshikawai*. The habit of every members of the Delesseriopsieae is similar though more slender than *Plumariella yoshikawai*, and the axes of unlimited growth of every genera are essentially corticated

with the branchlets produced on the basal segments of laterals. It is difficult to differentiate between indeterminate and determinate branches, but at least one species, *Balliella subcorticata*, of the tribe is quite identical with *Plumariella yoshikawai* by having indeterminate branches which replace one of the first-formed lateral branches in the pair that are distichously arranged. The contents of the tetrasporangia divide cruciately and the tetrasporangia are generally produced on the basal segments of the laterals and branchlets, or from the segmental cells of branchlets. These features of the tetrasporangia are quite similar to that of *Plumariella yoshikawai*; especially, those of *Balliella crouanioides* are quite identical with those of *Plumariella yoshikawai*.

Although I was unable to examine the female reproductive structure in the present study, *Plumariella yoshikawai* seems to have female reproductive structures similar to members of the Delesseriopsieae. Okamura (1930) reports briefly that the carposporophytes of this species as "cystocarps sessile on the side of branches, surrounded by many finger like involucre", and in reference to his figure (1930, pl. 268 fig. 11) maturation of the carposporophyte seems never to stunt the growth of the indeterminate axis which bears the carposporophyte. In *Balliella crouanioides* (Itono & Tanaka, 1973) and *Delesseriopsis elegans* (Itono, 1977), four-celled carpogonial branches are produced on the basal segments of the lateral branches, mature carposporophytes are surrounded with many involucre branchlets, and the mature carposporophytes are produced well behind the apex. *Dasyptilon pellucidum* (HARVEY) G. FELDMANN of the Ptiloteae is the species in which the procarps are produced on the proximal cells of the lateral branches and are inserted along the main axis towards the apex. They are not subterminal on side branches as they are in the Ptiloteae (Erskine, 1955; Hommersand, 1963). Although the arrangement of the procarps of *Dasyptilon* is similar to those of *Balliella* and *Delesseriopsis*, *Dasyptilon* is distinct by having procarps that are produced prior to the formation of the sterile group, and by the feature in which the maturation of the carposporophyte stunts the growth of indeterminate axis bearing carposporophyte.

These features as can be seen in *Balliella crouanioides* and *Delesseriopsis elegans*, as well as in *Plumariella yoshikawai*, may warrant the combination of these genera in the same group (tribe Delesseriopsieae) and, thus, *Plumariella* should be separated from the tribe Ptiloteae.

Some features of *Plumariella yoshikawai*, such as the transverse dividing apical cells, alternate-distichous arrangement of long and short lateral branches, indeterminate branches replacing the lateral branches, the cortical layers initiated by the progressive divisions of the proximal cells of the laterals, and so forth, are in common with some members of Ptiloteae. These features are, however, not the typical features of Ptiloteae, instead these features are frequently found entirely or partially in certain other members of Ceramiaceae.

Cruciately dividing tetrasporangium as can be seen in *Plumariella yoshikawai* is generally seen in Antithamnieae, Delesseriopsieae and some members of Ceramiaceae

(Itono, 1977), and is unfamiliar within the members of Ptiloteae. The contents of the tetrasporangium in most members of Ptiloteae divide tetrahedrally, and, thus, the cruciate divisions of tetrasporangia in *Plumariella* and *Plumariopsis* (De Toni, 1903) is peculiar among the members of Ptiloteae. The orientations of septa which divide the contents of tetrasporangia are frequently used as taxonomic criterion in the taxonomy of Rhodophyceae, and, in this respect, *Plumariella* and *Plumariopsis* should be separated from the Ptiloteae. However, little is known about *Plumariopsis*, and this genus should be retained tentatively under the tribe Ptiloteae.

*Dasyptilon* of the Ptiloteae is distinct by having distichous lateral branches, obliquely-dividing apical cell, presence of rhizoidal non-parenchymatous axial cortication, sessile tetrasporangia, and the production of procarps on the proximal cells of lateral branches (Erskine, 1955). Some of these features of *Dasyptilon* suggest that the generic assignment of this genus should be best placed somewhere near the Antithamnieae or even in the tribe Delesseriopsieae, but Erskine (1955) placed *Dasyptilon* under the tribe Ptiloteae based on the regular alternation of long and short lateral branches on the axis and on the production of carpogonial branch prior to the formation of the sterile group.

Based on the results obtained from the present study, *Plumariella* is very closely related to the members of Delesseriopsieae, and *Plumariella* should be provisionally placed under this tribe, until the details of the female reproductive structure are obtained, rather than placing the genus under the tribe Ptiloteae.

*Plumariella* is distinct from *Balliella* and *Delesseriopsis* of the Delesseriopsieae in the absence of gland cells and by the production of pseudoparenchymatous cortex. Vegetative structures of the members of Delesseriopsieae are generally related to both of Antithamnieae and of Ptiloteae, and it is suggested that, in the evolution of the Ptiloteae from the Antithamnieae, the members of the Delesseriopsieae might have linked these two tribes.

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