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Morphology of *Laurencia cartilaginea* Yamada (Rhodomelaceae, Rhodophyta)

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Abstract

Vegetative structure and reproductive organs of *Laurencia cartilaginea* Yamada were studied. Each axial segment, which is discernible only near the apex of branchlet, is provided with a trichoblast and two pericentral cells. Only in a tetrasporic plant, all of the axial cells show an addition of the pericentral cell number, as a result of the additional production of fertile pericentral cells; each of which produces a tetrasporangium. The first and second pericentral cells always remain sterile. Spermatangia are produced at trichoblast which is derived from an axial cell and the antherial trichoblast always consists of sterile and fertile branches. The second segment of the female trichoblast forms young procarys provided with five pericentral cells. The fifth of which always acts as the supporting cell. *L. cartilaginea* is easily distinguished from a similar species, *L. undulata* Yamada by the rostrated cystocarp and the conspicuous projection of epidermal cells at the distal end of ultimate branchlets.

Introduction

In spite of its long history (established by Lamouroux, 1813) the morphology of the genus *Laurencia* has not been well understood. Most of our knowledge on the morphology of this genus have been based essentially on the works of Falkenberg (1901), Kylin (1923, 1928) and Saito (1967). However, their works do not sufficiently clarify the morphology of the genus *Laurencia*. Moreover, there are even some questionable illustrations in their anatomy. This paper provides details of the anatomy of the vegetative structures and reproductive organs on *L. cartilaginea*. In addition, the differences between *L. cartilaginea* Yamada and *L. undulata* Yamada which have been confused in the past, are clarified on the basis of type specimen examination.

We express our sincere appreciation to Dr. R.T. Tsuda of the University of Guam, for critical reading of the manuscript.

Materials and Methods

Specimens of *L. cartilaginea* were collected from various sites along the coasts of Korea. The materials were preserved in 10 percent solution of formalin in seawater. For the anatomical examination, the liquid-preserved material was cleared in about 5 to 10 percent sodium hydroxide for 2 to 4 days, then rinsed in distilled water. The

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length of time depended on the concentration of the clearing reagent and the nature of materials. In the microscopic examination, sections were mainly used but squashed preparations were sometimes employed especially for the observation of the male organ. The sections were made by razor blade with the aid of a pith stick. For these sections, branchlets dissected from the cleared material were longitudinally split into two at a median position through the apex, and transferred on a slide with a drop of distilled water. The sections were mounted in pure glycerine. For the permanent preparation, the mounting medium was changed with 50 percent Karo corn syrup. Transverse sections of branchlets were also used, especially in the observation of young procarp, tetrasporangia and serial axial segments at vegetative structures. Branchlets with apical cells were transversely sectioned, about 50 to 200 μm or more in thickness, depending on the degree of clearing and the nature of the material. Only sections including apical cells were observed. In the preparation for the observation of axial segment of stichidium and sterile branchlets, the sections were reversed on the slide and mounted. The observation of the reversed sections was drawn and redrawn through tracing.

All of the sections were not stained, basically, in order to observe reproductive organs *in situ* through several cell layers.

Observations

General external appearance : Thalli are up to 10 cm or more high, and form coarse and compact clumps. Branches are terete or partly subcompressed to angular, sometimes slightly flattened when young. One or more erect axes arise from a discoid base, percurrent or not but rarely flexuous and usually are without basal stoloniferous branches.

Vegetative structure : The apical cell, sunk in the depression of the apex of branchlet, cuts off the axial cells successively in three faces which are slightly oblique. The resulting wedge-shaped axial segments are arranged along a 3/8 spiral; clockwise or counterclockwise (Fig. 1, A & C). Each of the axial segments produces a trichoblast and two pericentral cells (Fig. 1, A & B).

At first, the axial cell forms a protuberance at its upper side, and the protuberance is cut off obliquely when it comes to lie in about the third segment from the apex. The cut off protuberance acts as the basal cell of trichoblast. After that, the two pericentral cells are alternately produced from the axial cell. The first pericentral cell tends to be cut off laterally at its right or left rather than underneath the trichoblast initial. The second pericentral cell is produced at the opposite side

Abbreviations used in Figs. 1-5. a : axial cell (numbers 1, 2, ... indicates the sequence in the formation of axial cells). ap : apical cell. au : auxiliary cell. bs : basal sterile group. bsi : basal sterile group initial. bt : basal cell of trichoblast. c : central cell. cb : carpogonial branch (numbers 1, 2, ... indicates the cells of the carpogonial branch). cg : carpogonium. fb : fertile branch. fp : fertile pericentral cell. fu : fusion cell. gl : gonimolobe. ibi : indeterminate branch initial. ls : lateral sterile group. lsi : lateral sterile group initial. p : pericentral cell (numbers 1, 2, ... indicates the sequence in the formation of the pericentral cell). po : postsporangial cover cell. pr : presporangial cover cell. rh : rhizoid. sb : sterile branch. sbc : suprabasal cell of trichoblast. sg : sporangia. smt : spermatangium. stk : stalk cell. su : supporting cell. t : tetrasporangium initial. tb : trichoblast. tc : terminal sterile cell. ti : trichoblast initial.

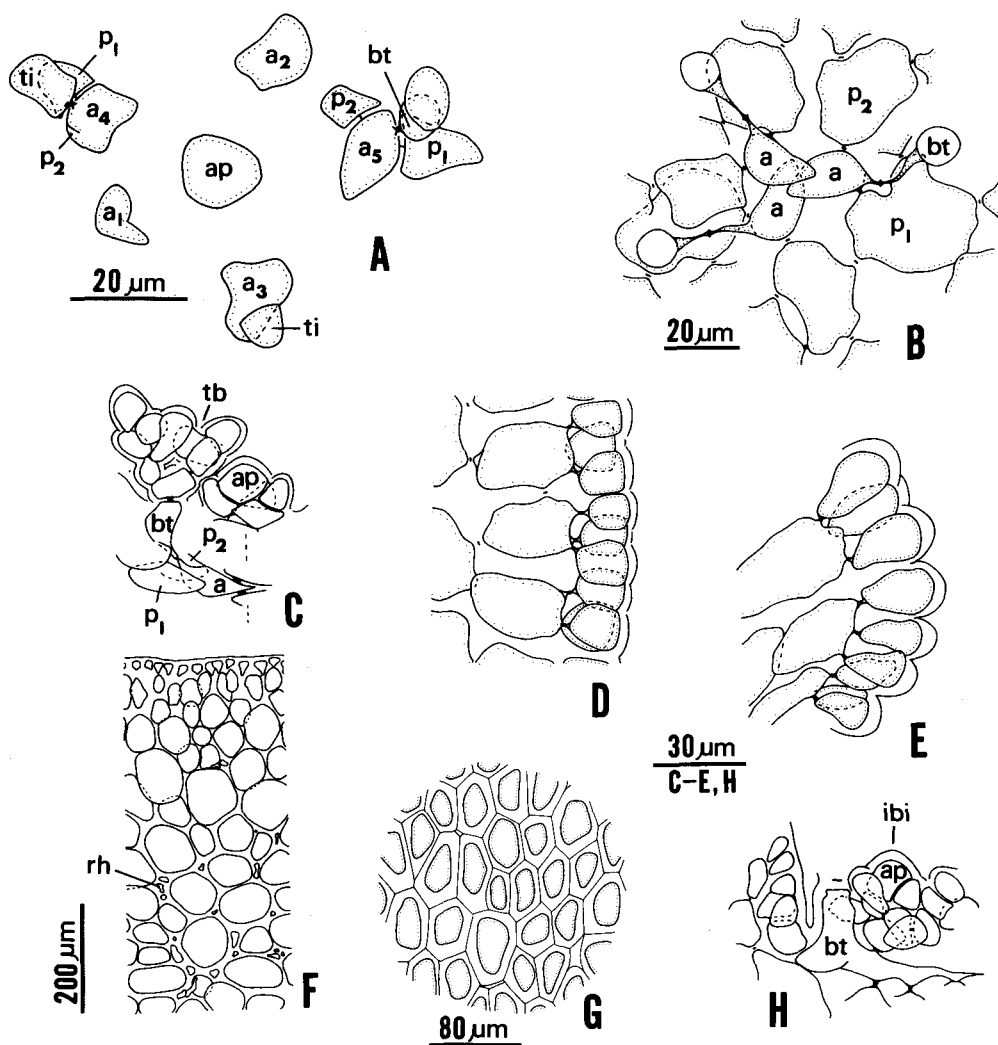


Fig. 1. *Laurencia cartilaginea* Yamada. A: Serial axial segments segregated in transverse section of a branchlet apex showing the sequence of formation of trichoblasts and the two pericentral cells. B: Transverse section near the apex of branchlet showing three axial segments, each of which is provided with a basal cell of trichoblast and two pericentral cells. C: Young trichoblast and axial cell with two pericentral cells in median longitudinal section through the apex of branchlet. D & E: Epidermal cells in transverse (D) and longitudinal (E) sections of branchlet. Note the dome projections of epidermal cells near the branchlet apex (E). F: Internal rhizoids growing among the medullary cells as seen in transverse section of main branch near the base. G: Surface view of a branchlet. H: Initial stage of indeterminate branch at the axilla of the basal cell of a trichoblast.

of the first. The first pericentral cell is always formed at the position closer to the trichoblast initial as compared with the second. Relative position of the two pericentral cells is determined by the spiral direction of axial segments. Namely, in the branch system of the clockwise spiral the first pericentral cell is always produced at the right of the trichoblast initial and at the left in the counter branch system. In a given branch system, their positions are invariably in all axial segments.

The pericentral cells usually produce three derivatives, each of which repeats the similar division several or more times to produce filaments of determinate growth. The filaments develop basically in a radial direction with some distortion, but sometimes in one plane, especially in young plant. The filaments form the pseudoparenchyma, while each cell, except the terminal cells, is connected by secondary pit connections with the adjacent cells of the filaments which are derived from the same and successive axial segment. This forms the cylindrical or compressed thallus of the inner condensed structure. However, this basic structure is discernible only near the apex of branchlets because of the abundant cortication that developed quickly with some distortion of the determinate filaments.

On the other hand, the young trichoblast continues to grow monopodially by producing two laterals subsequently on its suprabasal cell, while it is gradually displaced to the outside of apical depression with the development of the central axis. When it lies near the periphery of the depression, it is shed by abscission usually between the basal cell and suprabasal cell, and then leaves a scar among the epidermal cells. The scar, however, is later covered with adjacent epidermal cells.

Ordinary lateral branches arise from the axilla of the basal cells of the trichoblasts in the apical depression (Fig. 1, H). They are successively produced at regular or irregular interval. The regularity of the interval is directly related with the branching mode of the thallus. In the newly produced branches, the sequence of the development of the basic structure is the same as that described above. However, the spiral direction of the axial segments may be opposite to that in the parent branch system. The two counter spiral systems seem to occur by turn between daughter and parent branches.

The secondary cortication of rhizoidal filaments hardly occurs in the branches except at the base of the thallus. The internal rhizoidal filaments are sometimes observed among medullary cell (Fig. 1, F).

Epidermal cells are always projected conspicuously near the apex of the branchlet and do not form palisade-like layer in the transverse section of branchlet (Fig. 1, D & E, Fig. 7, G & H). Secondary pit connections are absent between the adjacent epidermal cells (Fig. 1, E & G, Fig. 7, I).

No lenticular thickenings are observable in the walls of medullary cells, however, the walls of medullary cells are usually thick (Fig. 1, F).

"*Corpse en cerise*" is detected in neither live materials nor the materials preserved in formalin seawater.

Development of the male reproductive organ : The apical depression of the branchlets in male plants is characteristically broadened since the apical cell ceases to divide and the determinate filaments grow rapidly (Fig. 6, D, Fig. 7, E). The resulting cup-shaped antheridial depression contains the numerous antheridial trichoblasts derived from the axial cells.

The antheridial trichoblasts always consist of fertile and sterile branches (Fig.

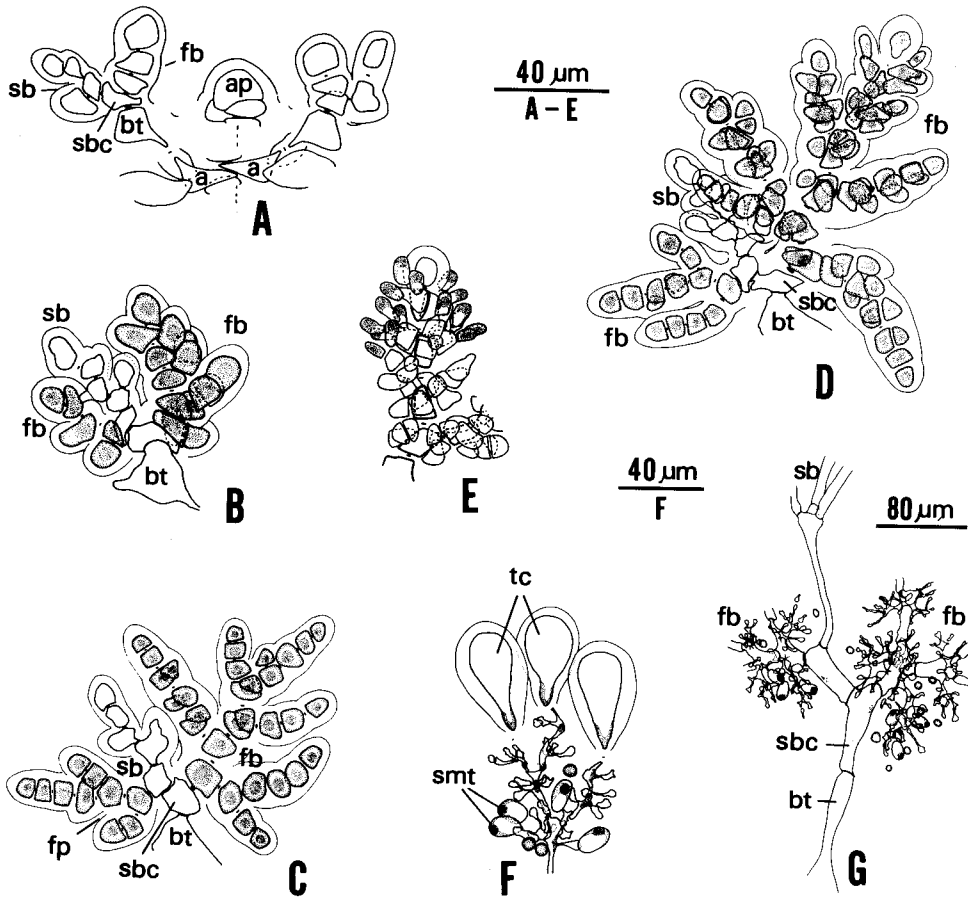
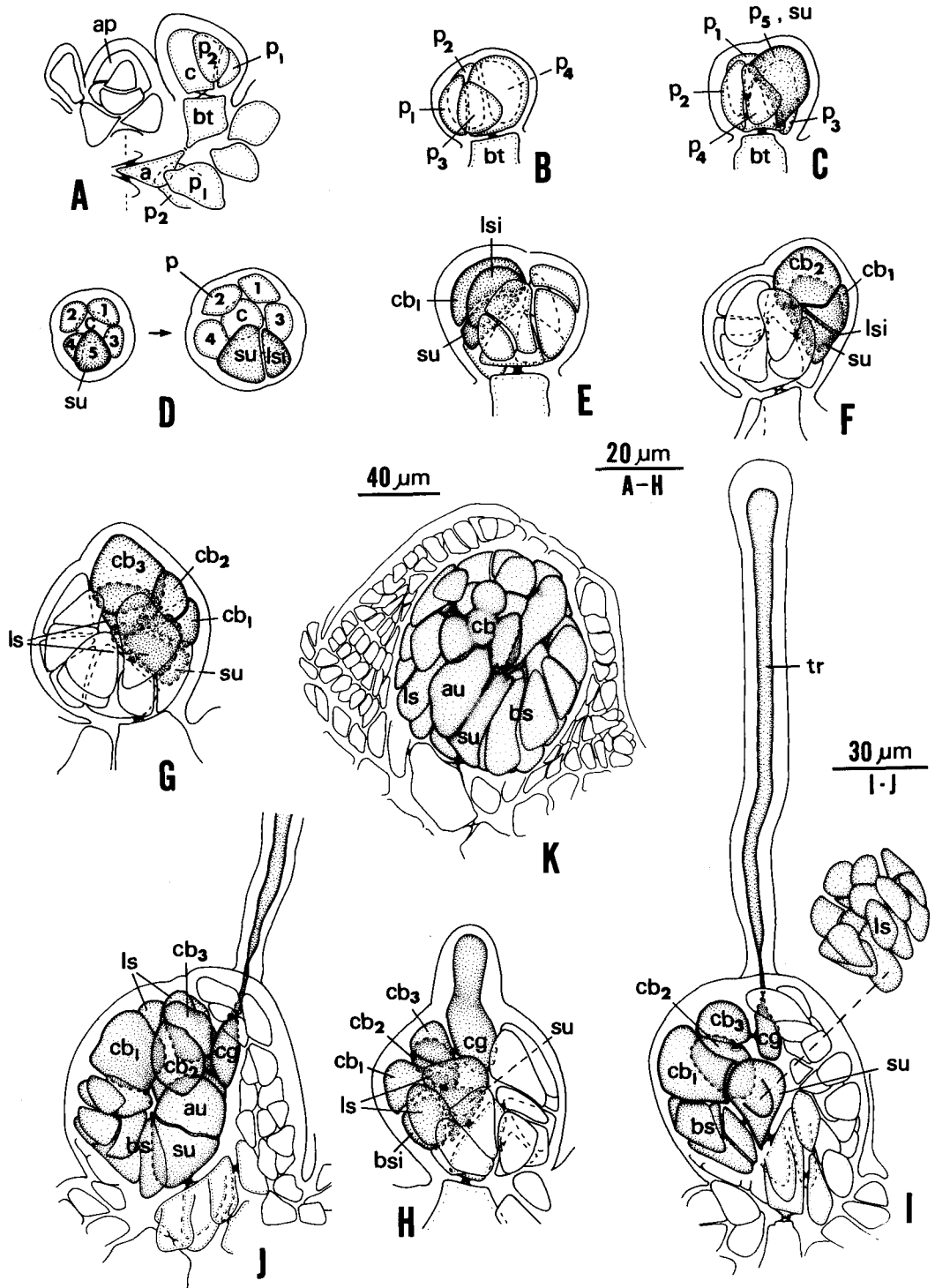


Fig. 2. *Laurencia cartilaginea* Yamada. A: Median longitudinal section through an antheridial depression, showing the young male trichoblasts derived from the axial cells. B-D: Several stages in the development of young antheridial trichoblasts, showing two kinds of laterals (sterile and fertile branches) on the suprabasal cell and partial formation of fertile branches on the sterile ones. E & F: Apical portion of young (E) and mature (F) antheridial trichoblasts, showing the terminal sterile large cells and spermatangia containing nucleus at the top. G: Old antheridial trichoblast partially formed as branches on a sterile branches.

2, B-D & G, Fig. 7, D). Of the two laterals on the suprabasal cell of the trichoblasts, one lateral on the adaxial side of the central axis develops into the fertile branches and the other into the sterile branches. This is presumably to protect the inner fertile branches on the outer side of the antheridial depression.

The fertile branches, of which the axial cells grow monopodially by subdichotomo-alternate branching, terminate in a single large pyriform sterile cell, about 49-58 μm long by 31-33 μm in diameter (Fig. 2, E & F, Fig. 7, F). Each of the axial cells cuts off pericentral cells which act directly or indirectly as spermatangial mother cells. The formation of the pericentral cells begins at about the third



or fourth segment from the suprabaasal cell of the trichoblast, and extends upward and downward to the successive segment (Fig. 2, C & D). All of the axial segments are clothed with the pericentral cells and their derivatives. Such sterile segments on the suprabaasal cell, as that in *L. venusta* Yamada (Nam, 1990, p. 71), are not formed in the present species (Fig. 2, G).

On the other hand, the sterile branches which are developed on the suprabaasal cell of the trichoblast, usually bear secondly the fertile branches on their basal segment (Fig. 2, G).

The spermatangial mother cell gives rise to several ovoid spermatangia, about 15–17 μm long by 9–10 μm in diameter, each of which bears a large apical nucleus (Fig. 2, F, Fig. 7, F). The contents are later liberated as a single spermatium.

Precise details of the number of the spermatangial mother cell and spermatangium have not been followed in this study. However, according to Saito (1967), they are produced in 4 and 1–3 (or more) per cell, respectively.

The cup-shaped antheridial depression is about 400–450 μm broad and up to 1.3 times as broad as deep.

Development of the female reproductive organ: Procarp occurs at the trichoblast in the apical depression of branchlet. The second segment (suprabaasal cell) of the trichoblast is always fertile (Fig. 3, A), and then produces five pericentral cells (Fig. 3, A–D). At that time the trichoblast is no more than two cells long, and never develops further in length, but remains as it is even later. The five pericentral cells are cut off in the alternating sequence of the typical rhodomelaceous order (Fig. 3, D, Fig. 7, H). The details of the formation of the five pericentral cells are the same as that of *L. obtusa* (Hudson) Lamouroux, described in Nam (1990). The fifth pericentral cell is finally produced and lying at the adaxial side, always functions as the supporting cell of the procarp.

The supporting cell first cuts off the initial cell of the first sterile group (lateral sterile group) at its lateral side, and then cuts off the carpogonial branch initial somewhat at the opposite side of the first sterile group (Fig. 3, D & E). The relationship of the position between the lateral sterile group initial and carpogonial branch initial is occasionally reversed. After that, the second sterile group (basal sterile group) initial is formed at the lower parts of the supporting cell, while the carpogonial branch initial develops into the two-cell stage (Fig. 3, H). Later, the carpogonial branch initial develops into the curved branch composed of four cells; the fourth cell, i. e., the carpogonium, lies adjacent to the upper parts of the supporting cell. The carpogonium produces a long trichogyne constricted at its

Fig. 3. *Laurencia cartilaginea* Yamada. A: A young procarp at the suprabaasal cell (fertile segment) of trichoblast as seen in a median longitudinal section through the apex of branchlet. B & C: Successive pericentral cells forming (finally into five) of the fertile segment of trichoblast. D: Young procarps as seen from the top of a branchlet, successive pericentral cell forming is as above, among them the fifth becomes supporting cell later; lateral sterile group initial is also observable. E: Next stage showing the initiation of carpogonial branch. F & G: Stage showing the development of carpogonial branch. H: Stage showing the four celled carpogonial branch and basal sterile group initial. I: Fully developed procarp before fertilization, showing a long trichogyne, four celled carpogonial branch, two sterile group cells and supporting cell. J: A procarp after fertilization, showing auxiliary cell cutting off from the supporting cell. K: Auxiliary cell fusing with supporting cell.

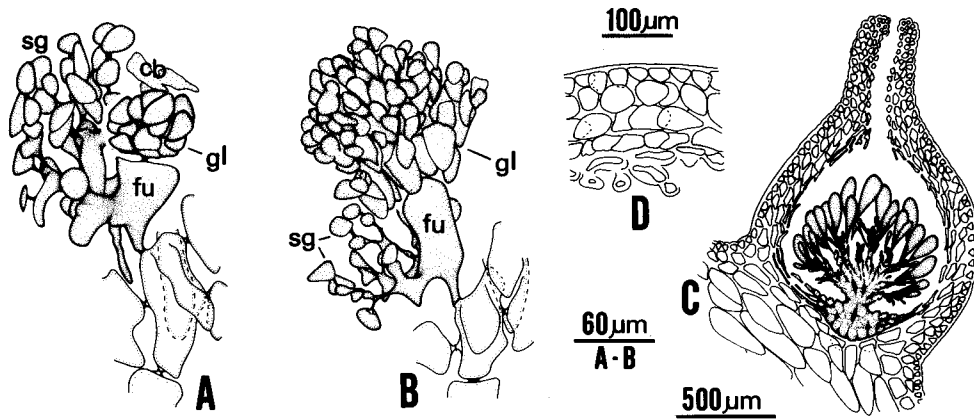


Fig. 4. *Laurencia cartilaginea* Yamada. A: Developing gonimoblasts on the fusion cell composed of auxiliary cell and supporting cell. B: More advanced stage in the development of gonimoblast; sterile cells are gradually disappearing with the development of gonimoblast. C: Median longitudinal section through a ripe cystocarp. D: Transverse section of pericarp consisting of 4-6 cell layers.

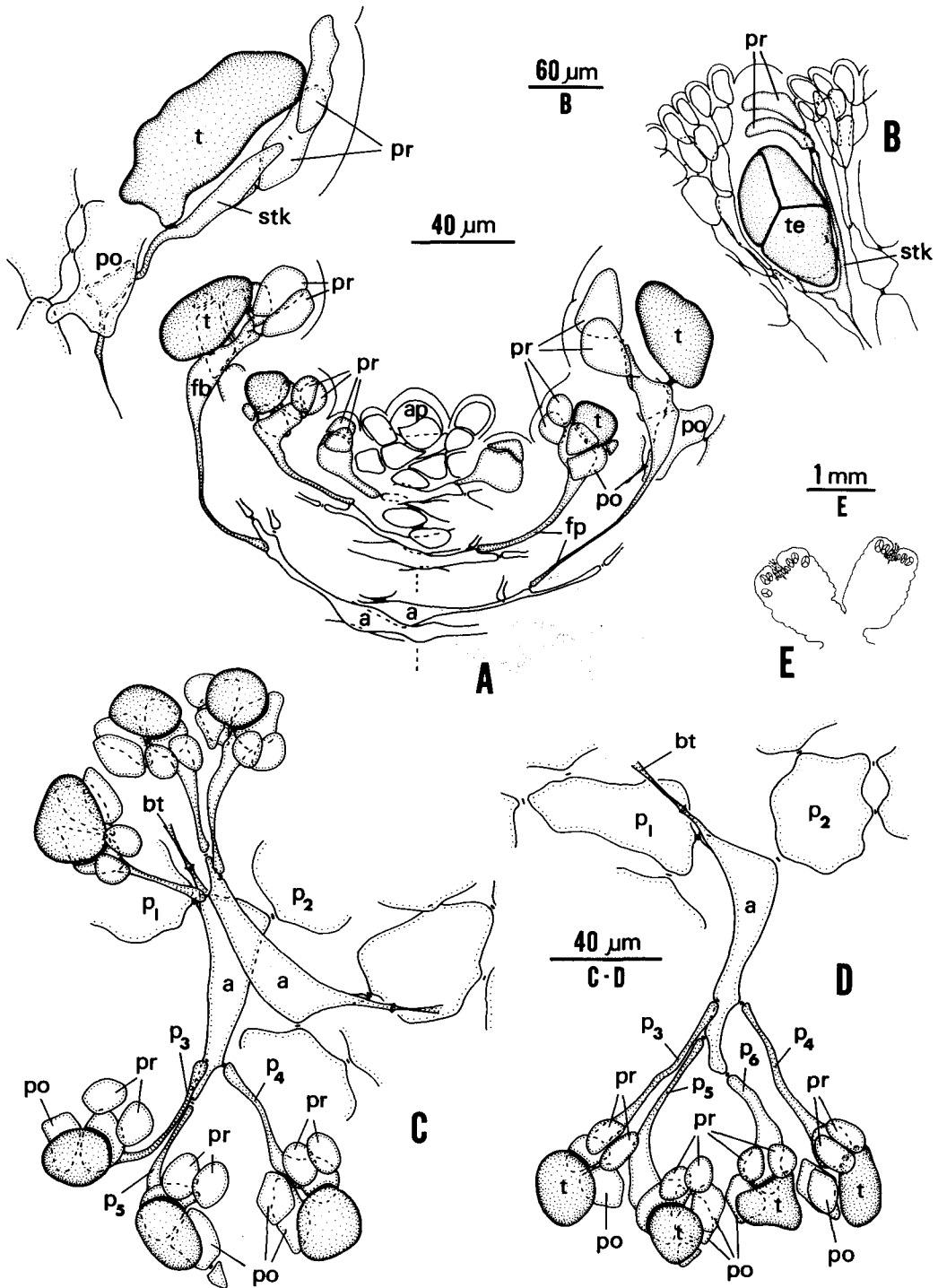
basal portion (Fig. 3, I).

Otherwise, at about the time of fertilization, the two sterile groups divide ternately or quaternary, producing about 2-3 cells and 5-6 cells, respectively.

An auxiliary cell is cut off from the distal end of the supporting cell after the presumed fertilization takes place (Fig. 3, J). The trichogyne is then separated from the carpogonium. It is usually cut at its basal constricted portion. Fusion occurs between the four cells of the carpogonial branch (Fig. 3, K). The resulting fusion cell, however, degenerates gradually with the development of gonimoblast (Fig. 4, A & B). Later, the auxiliary cell acting as the mother cell of the gonimoblast initial, enlarges remarkably with more dense cytoplasm in its contents, and fuse again gradually with the supporting cell (Fig. 3, K, Fig. 4, A & B).

While the two sterile group cells continue to divide, the gonimoblast initial is produced at the upper end of the auxiliary cell. At about this stage, the cells of the two sterile groups attain to the total of about 30-50 cells or more in number, and do not grow any more. The gonimoblast initial divides, forming the gonimoblasts of compacted mass in the early stage of the cystocarp (Fig. 4, A, Fig. 7, K), and their continuous division produces the numerous gonimoblast filaments (Fig. 4, B). Carposporangia are borne terminally and subterminally from the gonimoblast

Fig. 5. *Laurencia cartilaginea* Yamada. A: Median longitudinal section through the apex of a stichidium, showing various stages in the development of tetrasporangium and its cover cells; Note the postsporangial cover cells dividing and producing secondary pit connections. B: Divided tetrasporangium; postsporangial cover cell and its derivatives are undistinguishable from adjacent cells. C & D: Transverse section near the apex of stichidium, showing axial segments producing three or four fertile pericentral cells, all of which are additionally produced only for tetrasporangia; the first and second pericentral cells remain sterile. E: Tetrasporangia scattered near the apices of stichidia as seen in longitudinal section.



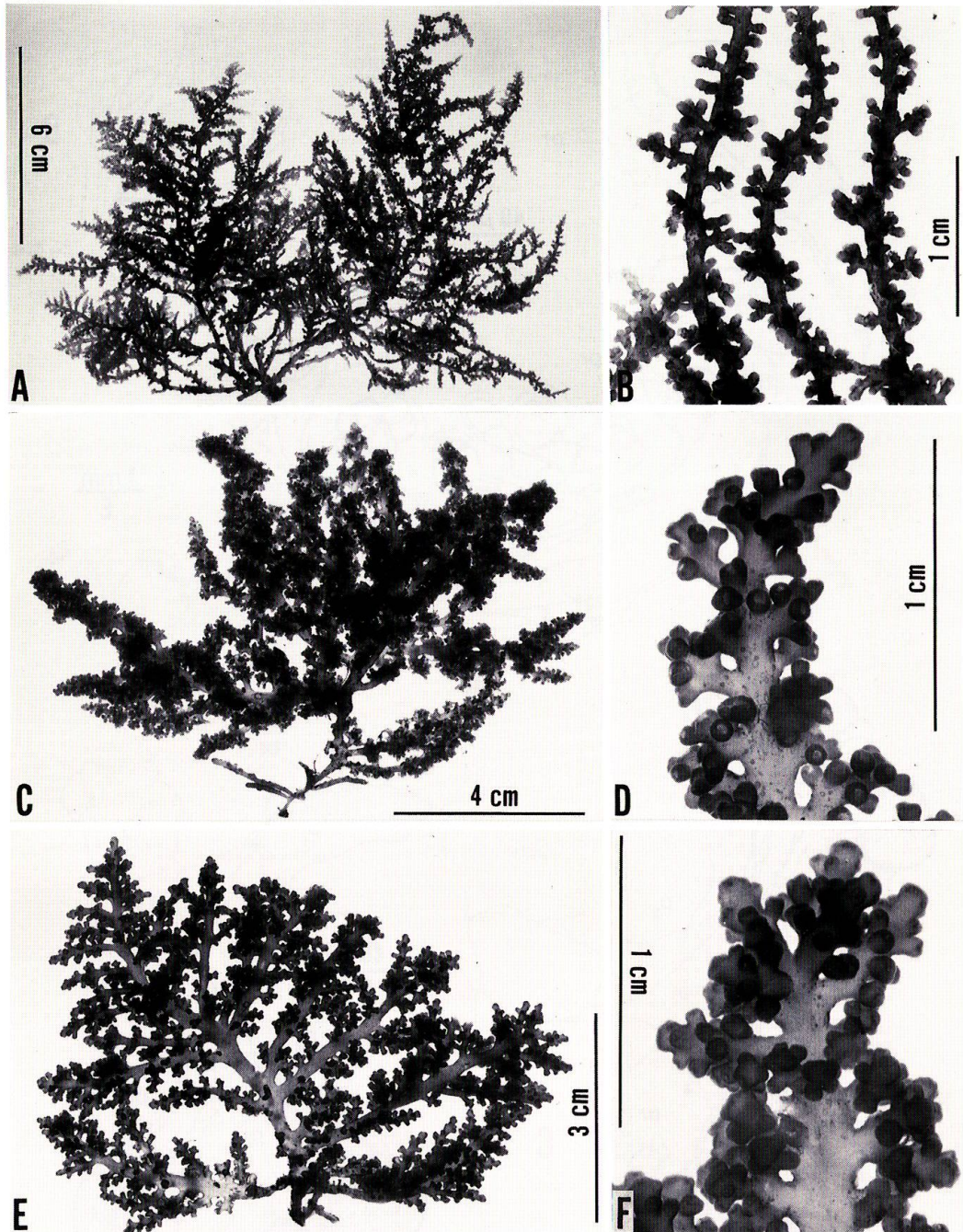


Fig. 6. *Laurencia cartilaginea* Yamada. A: Tetrasporic plant from Ilgwang near Pusan, Korea (25-IX-1983). B: Part of the tetrasporic plant. C: Male plant from Sungsanpo, Korea (19-VI-1986). D: Part of the male plant. E: Female plant from the same locality as that of Fig. C. F: Part of the female plant.

filaments. Mature carposporangia are clavate, about 190–230 μm long by 55–95 μm in diameter.

On the other hand, the fusion initiated between the auxiliary cell and the supporting cell is extended to the neighbouring cells. As a result, a large fusion cell is formed at the base of the cystocarp (Fig. 4, C).

The pericarp is produced from the four sterile pericentral cells of the fertile segment of the trichoblast. The formation of the pericarpic filaments is begun at early young procarpic stage (Fig. 3, E-H). The procarp, however, still remains naked partially before fertilization (Fig. 3, I). Each pericarpic filament continues to divide ternately or quaternately forming numerous secondary pit connections between adjacent cells derived from another pericarpic filaments. This produces the pseudoparenchymatous structure of the pericarp which consists of 4–6 cell layers in a fully developed cystocarp (Fig. 4, C & D). The pericarpic filaments build up rostrum of a ostiole especially in the upper parts of cystocarp (Fig. 4, C, Fig. 7, L & M). The mature cystocarps are conical, about 0.8–1.1 mm long by 0.6–0.8 mm in diameter, and lie at a distance from the apex since the axis of the indeterminate branch ordinarily continues to grow.

Development of the tetrasporangia : The pericentral cells of tetrasporangial branchlet produce tetrasporangia at their distal ends (Fig. 5, A, C & D). The usual production of the two derivatives (presporangial cover cells), before the formation of tetrasporangium initial, takes place at either sides of the upper parts of the fertile pericentral cells (Fig. 5, A). The two terminal derivatives remain undivided, growing only in size (Fig. 5, A & B). They act as the pair of cover cells (presporangial cover cells). Tetraspores presumably escape between those two when mature. Two presporangial cover cells are arranged by a width with respect to the direction of the axis in the surface view of stichidium, and do not form the secondary pit connections with adjacent epidermal cells. The third cover cell (postsporangial cover cell) which is cut off at the lateral side of the stalk cell after the tetrasporangium formation, divides further to produce the surrounding cortical and epidermal cells (Fig. 5, A). There are three to four fertile pericentral cells per axial segment in the stichidium, all of which are additionally produced for the tetrasporangia only in the stichidium. The number of fertile pericentral cells is more or less variable between different populations. However, the sterile pericentral cells are constantly two per axial segment. The first and second pericentral cells of the axial segment always remain as sterile ones and never become fertile ones (Fig. 5, C & D).

Mature tetrasporangia are immersed and scattered near the apical portion of the stichidium (Fig. 5, E, Fig. 7, N). They measure about 180–200 μm in diameter, and divided tetrahedrally.

Discussion

Since Kylin (1923), the number of pericentral cells of fertile segments of female trichoblast in this genus has been recognized as four. Saito (1967) also illustrated it in the present species. This observation, however, revealed that the fertile segment consists of five pericentral cells of which the fifth acts as the supporting cell of the procarp. Such procarp of five pericentral cell formation is common in this genus (Nam, 1990). Elsewhere, Saito's (1967) illustrations on reproductive organs of this



species are different from the present observation. We could not observe the procarps and antheridial trichoblasts arising from the pericentral cells. They always arose from the axial cell. On the other hand, Grubb (1925) suggested in *L. obtusa* that sterile and fertile trichoblasts, each of which is independent, occur together in an antheridial depression. However, as mentioned above, they do not occur independently in an apical depression, but do as a part of the antheridial trichoblasts. This is observed in the present species as well as in all species of trichoblast type of male organ (cf. "trichoblast type" in Nam, 1990). In the development of tetrasporangia, Saito's (1967) description also appears to have misinterpreted some aspects. According to the present observations, the presporangial cover cell, cut off from the fertile pericentral cell, was always in twos, and the third cover cell (postsporangial cover cell), which later develops into corticating system, was produced from the stalk cell (pericentral cell). The third cover cell was by no means produced from subcortical cells in the genus *Laurencia*.

The number of pericentral cells of the axial segment in *Laurencia* was mentioned only by Falkenberg (1901) and Kylin (1923). Falkenberg (1901) commented that there are three per axial cell. However, Kylin (1923) states that only two pericentral cells are produced from an axial cell in *L. pinnatifida* (Hudson) Lamouroux. We agree with the opinion of Kylin's since we could not find the formation of three pericentral cells (Nam, 1990). However, four pericentral cell formation is observed in some members of this genus (Nam, 1990). The present species represents the two pericentral cell type in all plants except tetrasporic plants. Only in tetrasporic plants, each axial segment produces additional tetrasporic cells each of which produces tetrasporangium. In all axial segments of the stichidium, the first and second pericentral cells always remain sterile and never develop into fertile ones. It differs from members of the section Palisadae in which only the first pericentral cell is sterile and the second always develops into the fertile one, in all axial segments of the stichidium (Nam, 1990).

Yamada (1931), after examining the specimens of *L. regia* J. Agardh in J. Agardh's herbarium, separated this taxon from one (No. 36696, from Hamilton Bay (Corée) miss Crouan) of the specimens of the species, and established it as a new species based on the specimen of Yendo's from Japan that is applicable to the specimen. According to his annotation at that time and the present observation, his

Fig. 7. *Laurencia cartilaginea* Yamada. A: Herbarium specimen of tetrasporic plant from Ilgwang near Pusan, Korea (25-IX-1983). B: Young antheridial trichoblast in smeared preparation, $\times 190$. C & F: Apical portion of young and mature antheridial trichoblasts, showing the pyriform terminal sterile cells (F) and spermatangia containing apical nucleus (C), $\times 380$ (C), $\times 190$ (F). D: Old antheridial trichoblast, showing two laterals (fertile and sterile) on the suprabasal cell (arrow); the partial formation of fertile branch on the sterile one, $\times 90$. E: Cup-shaped antheridial depression in longitudinal section, $\times 95$. G: Epidermal cells in longitudinal section of a branchlet, showing the dome projections, $\times 380$. H: Young procarp provided with five pericentral cells (arrowheads), as seen in the apex of branchlet, $\times 380$. I: Surface view of a branch, $\times 380$. J: Procarp (arrow) in longitudinal section of a branchlet apex, $\times 40$. K: Young cystocarp in longitudinal section, showing the development of gonimoblast (arrowhead), $\times 190$. L: Mature cystocarp with a rostrum in longitudinal section, $\times 30$. M: Branchlet with mature cystocarps, $\times 10$. N: Longitudinal section of stichidium, showing the tetrasporangia scattered near the apex, $\times 30$. O: Longitudinal section of branchlet from holotype specimen showing the dome projections of epidermal cells (arrowheads) near the apex of branchlet.

treatment of this species seems to be appropriate. Since that time, however, the present species has been confused with another of his species, *L. undulata*. The confusion is caused by the overlapping morphological variation of both species. As a matter of fact, the external appearance of both species approximates very much each other, at least in young stages of the development. Another reason for the confusion is insufficient original description and inaccuracies in the description of the decisive characters that distinguish them, i.e., in the present species surface cells are not projected in surface view (Yamada, 1931, p. 231). However, it became evident from the present examination of the type specimen that the present species shows considerable projection of surface cells (Fig. 7, G & O), whereas the other species, *L. undulata*, never shows projection of surface cells. The present observation of specimens for both species from Japan and Hawaii which Saito has retained also revealed the same results. However, Saito (1967) provided no comments as to this character. Moreover, he described the non-projecting superficial cortical cells in his Hawaiian species (Saito, 1969). Judging from figures, *L. undulata* sensu Saito (1967) seems to be referable to the present species. *L. undulata* sensu Nam & Kang (1984) is also to be treated as the present species. At any rate, this taxon is easily distinguished from *L. undulata* by the projection of surface cells and external appearance that occur at least in the old stage as shown in this study. Another difference between both species is the mature cystocarp. The present species produces rostrated cystocarp, whereas there is no rostrated cystocarp in *L. undulata*.

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