

## Developmental Morphology of *Osmundea crispera* (Ceramiales, Rhodophyta) from California

Ki Wan Nam\* and Han Gil Choi\*\*

Department of Marine Biology, Pukyong National University, Nam-gu Pusan 608-737, Korea

(Received March 1999, Accepted May 1999)

Developmental morphology of the red alga, *Osmundea crispera* (Hollenberg) Nam from California was studied on the basis of liquid-preserved and herbarium specimens. Vegetative axial segment of the species produces two pericentral cells and one trichoblast. Spermatangial filaments (branches) are derived from apical and epidermal cells in pocket-shaped apical pit with an ostiole-like upper opening. Procarp-bearing segment of female trichoblast produces five pericentral cells, of which the fifth functions as supporting cell of carpogonial branch. Tetrasporangial production occurs in random epidermal cells in apical pit of branchlets, and two presporangial cover cells show parallel arrangement to stichidial axis. As this vegetative and reproductive development is included in the generic delineation of *Osmundea* Stackhouse, *O. crispera* among the known *Osmundea* species is characterized by habit forming compact cushion-like clump with angular to terete thallus. It is also distinguished from *O. hybrida* (A.P. de Candolle) Nam without the compressed thallus by the number of pericentral cells in procarp-bearing segment and shape of spermatangial pit. Taxonomic implication of the shape of spermatangial pit is also included.

Key words: developmental morphology, red alga, *Osmundea crispera* (Hollenberg) Nam, California, taxonomy

### Introduction

The *Laurencia* Lamouroux (1813) complex (Ceramiales, Rhodophyta), with worldwide distribution from temperate to tropical regions, has been known as one of economic seaweeds (Abbott, 1986). In southeast Asia, Europe and other regions, it has been traditionally harvested for food, usually in the form of a salad of air dried and cooked with beans or with other vegetables (Zaneveld, 1956; Moreland, 1980; Calumpong, 1982). In some regions, it is used as a spices. Recently *Osmundea* Stackhouse (1809), which had been placed in *nomen rejiciendum* as an earlier facultative synonym of *Laurencia* (Papenfuss, 1947), was resurrected based on the male reproductive structure and tetrasporangial production (Nam et al., 1994).

This genus is delimited from *Laurencia* by the production of spermatangial filaments (branches) from apical and epidermal cells (filament type) rather than trichoblast (trichoblast type), and the production of tetrasporangia from random epidermal cells rather than particular pericentral cells (Nam et al., 1994). However, in superficial habit with apical cell sunk in branchlet apex, recognizable axial cell row only near apex and extensive cortex, both genera are inseparable from each other. This suggests that critical study of *Laurencia* complex from various localities is required in the context of the generic delimitation mentioned above.

*Osmundea crispera* (Hollenberg) Nam was established by Hollenberg in Smith and Hollenberg (1943, as *Laurencia crispera*) based on the male specimen (Type: Hollenberg No. 3003) collected from Pacific Grove. Since that its distribution has been reported only in Pacific coast of North America (Smith and Hollenberg, 1943; Smith,

\*To whom correspondence should be addressed.

\*\*Present address: Port Erin Marine Laboratory, The University of Liverpool, Port Erin, Isle of Man, UK

1944; Saito, 1969; Abbott and Hollenberg, 1976). Saito (1969) added some morphological informations to the species (as *Laurencia crispa*) as a member of "Spectabilis group". Recently Nam et al. (1994) provided new morphological informations of the species, and based on the work transferred the species to *Osmundea*. However, details of vegetative and reproductive morphology of the species were not included in their work.

In this study, details of developmental morphology of *Osmundea crispa* from California are studied, and compared to those of *O. hybrida* (A.P. de Candolle) Nam, which is considered to be associated with *O. crispa* in lacking the compressed thallus among the known *Osmundea* species. Taxonomic implication of the shape of spermatangial pit is also included.

### Materials and Methods

Data for this study were obtained from liquid-preserved and herbarium specimens collected from California. Methods for anatomical observation are the same as those given in Nam and Sohn (1994). Measurements are made as length  $\times$  diameter. Details of specimens examined are as follows: Mussel Point, California (Saito, 24.i.1967, S 601 sterile; Abbott, 7.v.1965, S860449; Abbott, 14.vi.1966, S9231 $\oplus$ , sterile; Abbott, 3.iv.1967, sterile; Abbott, 20.vi.1967, S9230 sterile; Saito, 18.viii.1978, S 860482  $\delta$ , S860481  $\phi$ , S860480 $\oplus$ ).

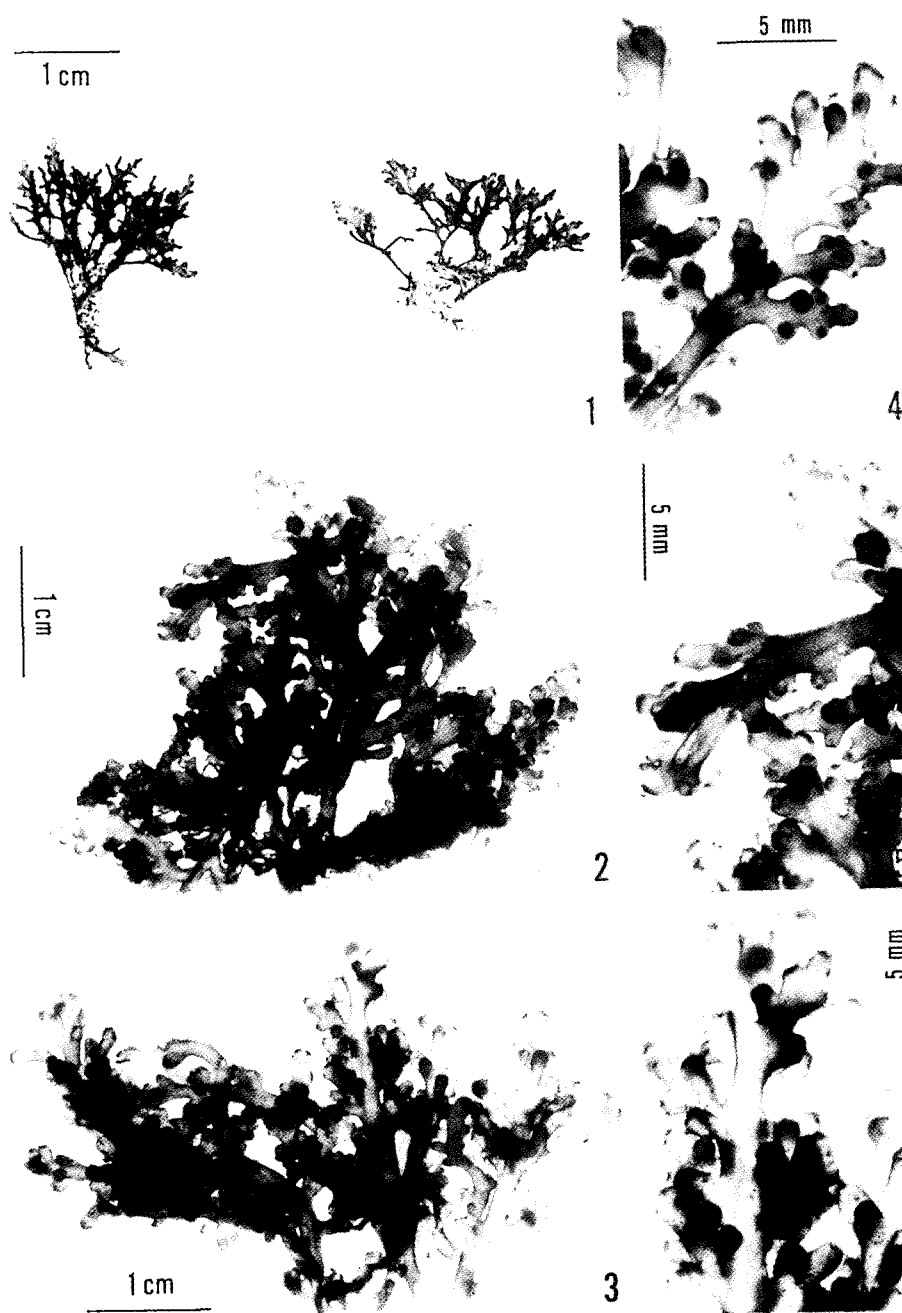
### Results and Discussion

**Habit:** Thalli are 3 to 10 cm high, angular to terete, occasionally partly slightly flattened (Figs. 1~6). Texture is fleshy and soft, adhering well to paper. Colour is brown or greenish brown, dark brown or purple on drying. Plants form compact cushion-like clump with many erect branches measuring 1.2~1.6 mm in diameter, and in the lower parts coalesced or intricate (Figs. 1~3). Branching is irregularly alternate, subopposite or distichous (Figs. 4~6). Ultimate branchlets are usually short with blunt tip, 0.7~0.9 mm in diameter. Male branchlets are shortly turbinate, 1.0~1.2 mm in diameter (Fig. 4). Tetrasporangial branchlets are simple and short with blunt tip, 0.9~1.3 mm in diameter (Fig. 6).

**Vegetative development:** Apical cell of branch tip cuts off wedge-shaped axial segments successi-

vely by oblique division with three faces (Fig. 7), and grows monopodially by this process. The axial segments are arranged along a  $3/8$  spiral, clockwise or counterclockwise (Figs. 7, 8). Each axial cell produces a trichoblast and two pericentral cells (Fig. 8). The trichoblast initial is first cut off obliquely through protuberance at upper side of axial cell. Subsequently, the two pericentral cells are produced at both sides of the trichoblast initial (Fig. 7). This basic structure and development of the thallus are recognizable only near branchlet apex, as in *Laurencia* (Nam and Sohn, 1994; Nam et al., 1994; Nam and Saito, 1995; Fujii and Cordeiro-Marino, 1996; Masuda et al., 1996). Each pericentral cell divides ternately or quaternately, then develops into many determinate filaments, which later give rise to pseudoparenchymatous structure of the thallus through formation of numerous secondary pit connections between adjacent cells except for axial cell. On the other hand, the trichoblast initial grows by subdichotomo-alternate branching, forming a dense bunch in the apical pit. However, fully developed trichoblast sheds near periphery of the apical pit, and leaves vestigial scar among epidermal cells in upper parts of the branchlet (Fig. 10). However, the scar is buried under epidermal cells, later. New lateral branches are formed at axils of the trichoblast basal cell (Fig. 9), and grow indeterminate. They are successively produced in radial direction. Basic structure of the branches is the same as that described above, probably except for spiral direction of arrangement of axial segments. Unlike in *Osmundea hybrida* (Nam and Saito, 1994, as *Laurencia hybrida*), secondary cortication by rhizoidal filaments hardly occurs in branches. Secondary pit connections are not observed between epidermal cells (Figs. 10~12). The epidermal cells are neither elongated radially nor arranged like palisade cells in transverse section of branchlet and are not protruded (Fig. 11). There are no lenticular thickenings in walls of medullary cells. *Corps en cerise* were not examined in live materials.

**Reproductive development:** Male branchlet produces a pocket-shaped pit at its apex. The pit contains numerous spermatangial filaments derived from apical and epidermal cells (Figs. 13, 14). The spermatangial filaments occasionally branch alternately, and terminate in several large vesicular sterile cells in the pocket-shaped pit



Abbreviations in Figs 1~20. a, axial cell; ap, apical cell; au, auxiliary cell; bs, basal sterile group; bsi, basal sterile group initial; bt, basal cell of trichoblast; central cell of procarp-bearing segment; cb, carpogonial branch; cg, carpogonium; cj, conjuctor cell; ep, epidermal cell; gi, gonimoblast initial; ibi, indeterminate branch initial; is, lateral sterile group; lsi, lateral sterile group initial; sc, scar of trichoblast after shedding; p, pericentral cell; po, postsporangial cover cell; pr, presporangial cover cell; sg, sterile group; sp, spermatangial filament; spi, spermatangial filament initial; stk, stalk cell; su, supporting cell; tc, terminal vesicular sterile cell; te, tetrasporangium; ti, trichoblast initial; tr, trichogyne; 1, 2 etc., formation sequence

Fig. 1~6. Habit of *Osmundea crista* (Hollenberg) Nam

Fig. 1. Herbarium mounted female plants from Mussel Point, California.

Fig. 2. Liquid-preserved female plant.

Fig. 4. Details of male branches.

Fig. 6. Details of tetrasporangial branches.

Fig. 3. Tetrasporangial plant.

Fig. 5. Details of female branches.

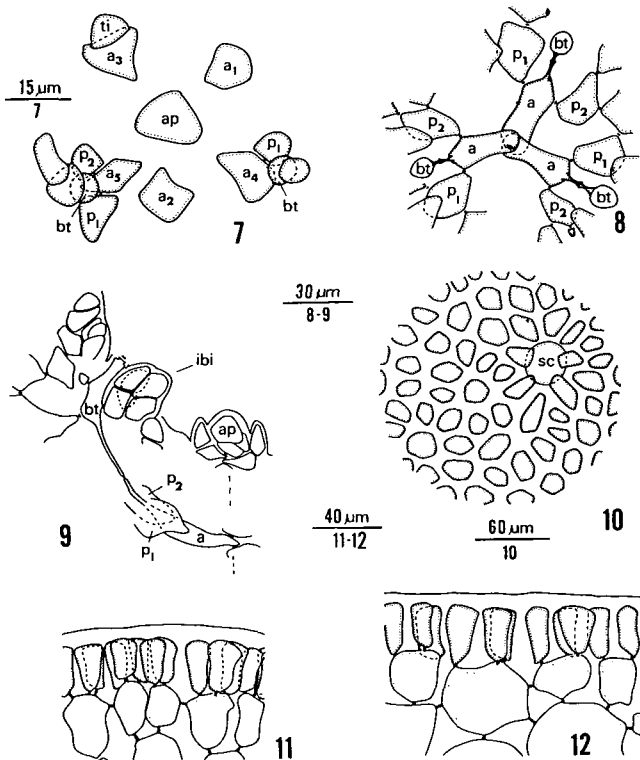


Fig. 7~12. Vegetative structure of *Osmundea crisper* (Hollenberg) Nam  
 Fig. 7. Successive axial segments.  
 Fig. 8. Three superimposed vegetative axial segments.  
 Fig. 9. New lateral branch initial at axilla of trichoblast basal cell.  
 Fig. 10~12. Epidermal cells in surface view (Fig. 10), transverse (Fig. 11) and longitudinal (Fig. 12) section of branchlet.

with an ostiole-like upper opening, as in *Osmundea spectabilis* (Nam et al., 1994). The terminal cells are  $17\sim 24 \times 15\sim 18 \mu\text{m}$ . Each axial cell of spermatangial filaments cuts off some pericentral cells functioning directly or indirectly as spermatangial mother cells, forming a continuous layer of spermatangial mother cells around it. The spermatangial mother cell gives rise to several ovoid spermatangia with an apical nucleus,  $8\sim 10 \times 5\sim 6 \mu\text{m}$ . The nucleus is liberated with contents of the spermatangium as a single spermatium, later. The pocket-shaped spermatangial pit fully developed is  $650\sim 750 \mu\text{m}$  broad by  $800\sim 850 \mu\text{m}$  deep.

Procarp is produced from the second segment (suprabasal cell) of trichoblast in apical pit of branchlet (Fig. 15). The suprabasal cell of the trichoblast cuts off five pericentral cells in the rhodomelaecous sequence (Fig. 16). The fifth pericentral cell

finally produced nearly at adaxial side acts as supporting cell of carpogonial branch (Fig. 16). The supporting cell first cuts off lateral sterile group initial (Fig. 16). The lateral sterile group initial is formed on the side facing the fourth pericentral cell, and then the initial of the carpogonial branch is cut off at upper part of the side slightly facing the third pericentral cell (Fig. 16). Occasionally, the formation position of the lateral sterile group initial and the carpogonial branch initial is reversed. The carpogonial branch initial divides into three cells. At about that time, the supporting cell cuts off initial of basal sterile group below the carpogonial branch initial. The carpogonial branch initial develops into four-celled branch, and the fourth cell becomes carpogonium, giving a long trichogyne upward. Otherwise the two sterile groups give respectively 6~7 cells and 3~4 cells by ternate or quaternate division, at the time of fertilization. After presumed fertilization, auxiliary cell, together with shedding of trichogyne, is produced from upper end of the supporting cell (Fig. 17). Later, the four cells of carpogonial branch are fused with each other. Then they degenerate gradually, eventually disappear (Fig. 17). On the other hand, the cells of two sterile groups continue to grow, increasing considerably in number and size until development of gonimoblasts starts, eventually attaining to a total of 25~30 cells (Fig. 17). They also become more densely cytoplasmic in content. At about this stage, cavity of cystocarp is almost filled with them. The auxiliary cell, which enlarges gradually, is fused with the supporting cell, and then functions as mother cell of gonimoblast initial. The gonimoblast initial produced from upper end of the auxiliary cell develops into compacted mass in early stage of cystocarp. However, it continues to divide sympodially, giving a number of gonimoblast filaments, from which carposporangia are produced terminally and subterminally. Mature carposporangia are clavate,  $180\sim 200 \times 30\sim 40 \mu\text{m}$ . With the development of gonimoblasts, the sterile group cells disappear gradually since their content is absorbed as the presumed nutrition for growing of the gonimoblasts. Instead, gonimoblasts replace the space occupied by them. On the other hand, the fusion initiated between the auxiliary cell and the supporting cell is extended to the neighbouring cells, such as axial cell of fertile segment, parts of sterile pericentral cell and gonimoblasts in the lower parts. Consequently a large fusion cell, of

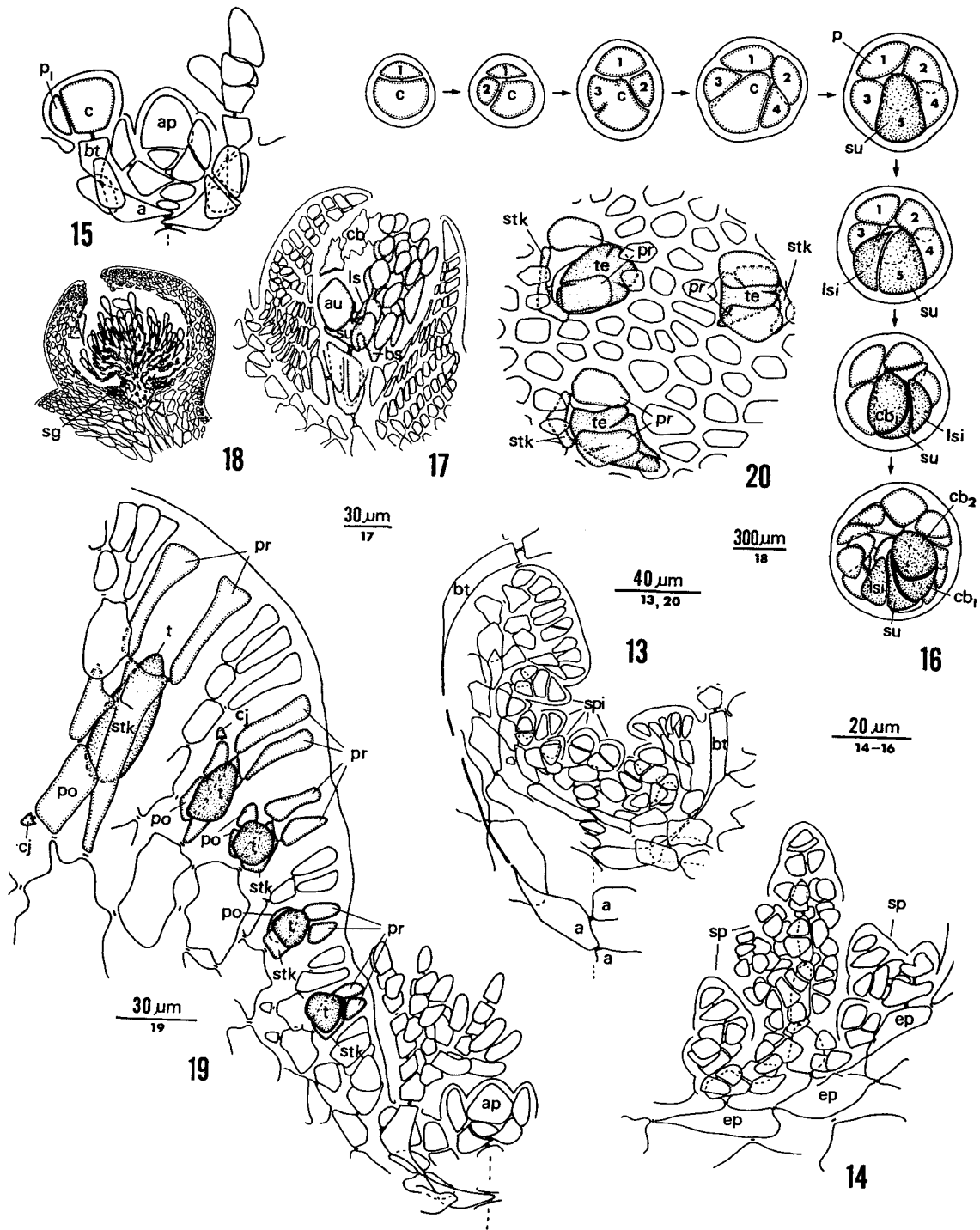


Fig. 13~20. Reproductive structure of *Osmundea crispata* (Hollenberg) Nam

Fig. 13. Initial of spermatangial filaments arising from apical and epidermal cells in apical pit of branchlet.

Fig. 14. Young spermatangial filaments from epidermal cells.

Fig. 15. Young procarp seen in median longitudinal section of branchlet.

Fig. 16. Sequential stage of the development of young procarp as seen from branchlet apex.

Fig. 17. Procarp after presumed fertilization.

Fig. 18. Mature cystocarp.

Fig. 19. Development of tetrasporangia from random epidermal cells in median longitudinal section of branchlet.

Fig. 20. Tetrasporangia and cover cells in surface view of branchlet.

which upper part produces subsequently additional gonimoblasts, is formed at the base of the cystocarp. Filaments of determinate growth, which are derived from the sterile pericentral cells, build up pseudoparenchymatous pericarp. Their development for pericarp production is begun with formation of procarp. However, procarp remains still partly naked, usually in part of carpogonial branch and lateral sterile group at about the time of fertilization. The pericarpic filaments continue to divide ternately or quaternately with establishment of numerous secondary pit connections between adjacent cells, so that ultimately cover fully the cystocarp except for ostiole. The pericarp is composed of 4~6 cell layers in fully developed cystocarp. Mature cystocarps are ovoid to subconical,  $1000\sim 1300\times 1100\sim 1300\ \mu\text{m}$ , slightly constricted at base, without protrusion of ostiole (Fig. 18).

Tetrasporangia are produced in ultimate branchlets. Tetrasporangial initials are randomly borne on epidermal cells near apical cell of branchlet (Fig. 19). The fertile epidermal cells, however, are usually not distinguishable from sterile ones until two presporangial cover cells are formed. The first presporangial cover cell is always cut off by oblique division toward the abaxial side to central axis of the branchlet, and then the second toward the adaxial side (Fig. 19). In consequence of the division, a pair of the presporangial cover cells is arranged parallel to stichidial axis in surface view (Fig. 20). After that time, the fertile epidermal cell divides longitudinally by concave septum, producing the tetrasporangium initial at its lateral side and a residual stalk cell (Fig. 19). Subsequently the stalk cell cuts off the third cover cell (postsporangial cover cell). The postsporangial cover cell divides one or two (more?) times, and its derivatives are connected with adjacent cells by secondary pit connections (Fig. 19), producing a corticating system around the developing tetrasporangium. On the contrary, the two presporangial cover cells remain as undivided, forming a pair of large cells (Figs. 19, 20). In accordance with continuous growing of the branchlet, the tetrasporangia are gradually displaced out side of apical pit, eventually dispersed in lateral sides of the branchlet. Mature tetrasporangia with tetrahedral division reach  $100\sim 130\ \mu\text{m}$  in diameter (Fig. 20).

As described above, male reproductive structure shows the "filament type" and tetrasporangial

productions occur in random epidermal cells, which are of the generic criteria of *Osmundea*. Other vegetative and reproductive developments are also essentially the same as those of the previously examined species of *Osmundea* (Furnari and Serio, 1993a, 1993b; Cormaci et al., 1994; Nam et al., 1994) except for procarpic development of *O. hybrida* (Nam and Saito, 1994).

Since Nam et al. (1994), 14 species have been reported in the genus *Osmundea*, such as *O. osmunda* (S.G. Gmelin) Nam et Maggs, *O. spectabilis* (Postels et Ruprecht) Nam, *O. crispa* (Hollenberg) Nam, *O. splendens* (Hollenberg) Nam, *O. blinksii* (Hollenberg et Abbott) Nam, *O. multibulba* (Dawson, Neushul et Wildman) Nam, *O. spectabilis* var. *diegoensis* (Dawson) Nam, *O. sinicola* (Setchell et Gardner) Nam, *O. pinnatifida* (Hudson) Stackhouse, *O. hybrida* (A.P. de Candolle) Nam, *O. truncata* (Kützing) Nam et Maggs, *O. pelagosae* (Schiffner) Nam, *O. pelagiensis* (Cormaci, Furnari et Serio) Furnari, and *O. verlaquei* (Cormaci, Furnari et Serio) Furnari. Most of them have the strongly compressed thallus except near the base of axes, usually resulting in distichous branching. However, *O. crispa* shows angular to terete thallus, even though occasionally has partly slightly flattened thallus. *O. hybrida* also lacks the compressed thallus as *O. crispa* (Saito, 1982; Maggs and Hommersand, 1993; Nam and Saito, 1994), but both species differ from each other. While the former species has six pericentral cells in procarp-bearing segment of female trichoblast (Nam and Saito, 1994), the latter produces five ones in the segment. By the habit, *O. crispa* is distinguished from *O. hybrida*. As stated in Hollenberg's (in Smith and Hollenberg, 1943) original description (as *Laurencia crispa*), *O. crispa* is characterized by habit forming the compact cushion-like clump with angular to terete thallus.

The 14 reported species can be divided by shape of spermatangial pit into two groups, *O. osmunda* group and *O. hybrida* group. As the former group has the pocket-shaped spermatangial pit with an ostiole-like upper opening, including *O. osmunda*, *O. spectabilis*, *O. crispa*, *O. splendens*, *O. blinksii*, *O. multibulba*, *O. spectabilis* var. *diegoensis*, *O. sinicola*, *O. pinnatifida* and probably *O. pelagosae* (Saito, 1969; Maggs and Hommersand, 1993; Furnari and Serio, 1993a; Nam et al., 1994; Cormaci et al., 1994). The other group involves *O. hybrida*, *O. truncata*, *O. verlaquei* and *O. pelagiensis*

(Saito, 1982; Maggs and Hommersand, 1993; Furnari and Serio, 1993b; Nam and Saito, 1994; Cormaci et al., 1994), which produce the cup-shaped spermatangial pit. *Osmundea crispera* is also readily distinguished from *O. hybrida* by this spermatangial feature. In future, this character of shape of spermatangial pit may provide a basis for infrageneric taxonomy of *Osmundea*.

### Acknowledgements

We would like to thank Professor Y. Saito (retired from Hokkaido University, Japan) for providing the specimens. Thanks are also due to Miss S. Lee for her assistance in preparing the manuscript. This study was supported by grant No. KOSEF 961-0509-072-1 from the Basic Research program of the KOSEF.

### References

- Abbott, I.A. 1986. Taxonomy of economic seaweed with reference to some Pacific and Caribbean species Volume II. 264 pp.
- Abbott, I. A. and G.J. Hollenberg. 1976. Marine algae of California. Stanford Univ. Press. 827 pp.
- Calumpang, H. P. 1982. Economically important species of benthic marine algae in Central Visayas, Philippines. *Silkima J.* 28, 143~148.
- Cormaci, M., G. Furnari and D. Serio. 1994. Two new species of *Laurencia* (Ceramiales, Rhodophyta) from the Mediterranean Sea: *Laurencia pelagiensis* sp. nov. and *Laurencia verlaquei* sp. nov., *Jpn. J. Phycol.*, 42, 365~375.
- Fujii, M.T. and M. Cordeiro-Marino. 1996. *Laurencia translucida* sp. nov. (Ceramiales, Rhodophyta) from Brazil. *Phycologia*, 35, 542~549.
- Furnari, G. and D. Serio. 1993a. The reproductive structure of the Mediterranean alga *Laurencia pelagosae* (Ceramiales, Rhodophyta). *Eur. J. Phycol.*, 28, 141~143.
- Furnari, G. and D. Serio. 1993b. The distinction of *Laurencia truncata* (Ceramiales, Rhodophyta) in the Mediterranean Sea from *Laurencia pinnatifida*. *Phycologia*, 32, 367~372.
- Maggs, C.A. and M.H. Hommersand. 1993. Seaweeds of the British Isles. vol. 1. Rhodophyta, part 3a. Ceramiales. Natural History Museum, London. xv+444pp.
- Masuda, M., T. Abe, T. Suzuki and M. Suzuki. 1996. Morphological and chemotaxonomic studies on *Laurencia composita* and *L. okamurae* (Ceramiales, Rhodophyta). *Phycologia*, 35, 550~562.
- Lamouroux, J. V. 1813. Essai sur les genres de la famille des Thallasiophyte non articulées. *Ann. du Mus. d'Hist. Nat. Paris*, 20, 21~47, 115~139, 267~293, pls. 5~13.
- Moreland, P.S. 1980. Edible seaweeds of Northern Luzon, Philippines: market prices, local taste preferences, seaweed recipes and other local uses. *The Philipp. J. Sci.*, 108, 41~53.
- Nam, K.W., C.A. Maggs and D.J. Garbary. 1994. Resurrection of the genus *Osmundea* with an emendation of the generic delineation of *Laurencia* (Ceramiales, Rhodophyta). *Phycologia*, 33, 384~395.
- Nam, K.W. and Y. Saito. 1994. A re-examination of *Laurencia hybrida* (Ceramiales, Rhodophyta) from the British Isles: vegetative and reproductive morphology. *Phycologia*, 33, 34~41.
- Nam, K.W. and C.H. Sohn. 1994. *Laurencia kangjaewonii* sp. nov. (Ceramiales, Rhodophyta) from Korea. *Phycologia*, 33, 397~403.
- Nam, K.W. and Y. Saito. 1995. Vegetative and reproductive anatomy of some *Laurencia* (Ceramiales, Rhodophyta) species with a description of *L. marisrubri* sp. nov. from the Red Sea. *Phycologia*, 34, 157~165.
- Papenfuss, G.F. 1947. Generic names of algae proposed for conservation. I. *Madroño*, 9, 8~17.
- Saito, Y. 1969. On morphological distinctions of some species of Pacific North American *Laurencia*. *Phycologia*, 8, 85~90.
- Saito, Y. 1982. Morphology and infrageneric position of three British species of *Laurencia* (Ceramiales, Rhodophyta). *Phycologia*, 21, 299~306.
- Smith, G.M. 1944. Marine algae of the Monterey Peninsula California. Stanford Univ. Press. 752pp.
- Smith, G.M. and G.J. Hollenberg. 1943. On some Rhodophyceae from the Monterey Peninsula, California. *Amer. Jour. Bot.*, 30, 211~222.
- Stackhouse, J. 1809. *Tentamen marino-cryptogamicum*, *Mem. Soc. Imp. Nat. Moscou*, 2, 50~97.
- Zaneveld, J.S. 1956. The economic marine algae of the tropical regions of south and east Asia and their utilization. Indo-Pacific Fish. Council. (FAO) Sp. Publ. No. 3, 55 pp.