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Dasysiphonia chejuensis gen. et sp. nov. (Rhodophyta, Dasyaceae) From Korea

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Abstract. *Dasysiphonia chejuensis* gen. et sp. nov., a marine red alga belonging to the Dasyaceae, Ceramiales, is described from Cheju Island on the southern coast of Korea. The thallus grows sympodially, forming an indeterminate or determinate branch from every segment of main axes in bilateral-dorsiventral manner, and bears five pericentral cells derived alternately from each central cell. The main axes are lightly corticated. Spermatangial branches and tetrasporangial stichidia develop on monosiphonous determinate branches. Tetrasporangia are not completely protected by cover cells. Procarps bearing two sterile groups occur alternately in successive segments on specially developed polysiphonous fertile branchlets. The second or third pericentral cell adjacent to the first always becomes the supporting cell. The new genus morphologically resembles *Heterosiphonia* in its lateral-dorsiventral branch system, but is also similar to *Dasya* especially in tetrasporangium formation.

At present the Dasyaceae (Ceramiales) is comprised of eleven genera which occur mainly in warm temperate marine regions, particularly Australia (Kylin, 1956; Parsons, 1975). Most genera are monotypic or consist of only a few species except for *Dasya* C. Agardh (perhaps 70 species), *Dasyopsis* Zanardini (about 10 species) and *Heterosiphonia* Montagne (about 40 species). In Korea only two species of *Heterosiphonia* and four species of *Dasya* are recorded from southern and eastern coasts affected by the Kuroshio current (Kang, 1966).

From an island located on the southern coast of Korea (Fig. 1), we collected tetrasporic and procarpic plants of a red alga belonging to the Dasyaceae. They resembled *Heterosiphonia* in vegatative morphology, but appeared more related to *Dasya* in reproductive morphology.

The vegetative and reproductive structures of these plants do not accord with any previously described genus. A new monotypic genus is therefore proposed to receive this new species.

Dasysiphonia Lee and West, gen. nov.

Frons erecta, sympodialis in incrementum, ramum indeterminatum vel determinatum ex omni segmento axium principalium in modo bilaterali et dorsiventrali formans, per hapteron rhizoideum affixa; axes principales corticantes laete polysiphonibus, 5 cellulas pericentrales e cellulis centralis alterne efficientes; rami indeterminati aliquot ordines ramorum lateralium in ordinatione eodem ac in axibus principalibus efferentes; rami determinati monosiphonibus 1-vel 3-plo per incrementum sympodiale dividentes, in fila capilliformia in thallis veterioribus et ramulis femineis fertilibus transmutati; stichidia

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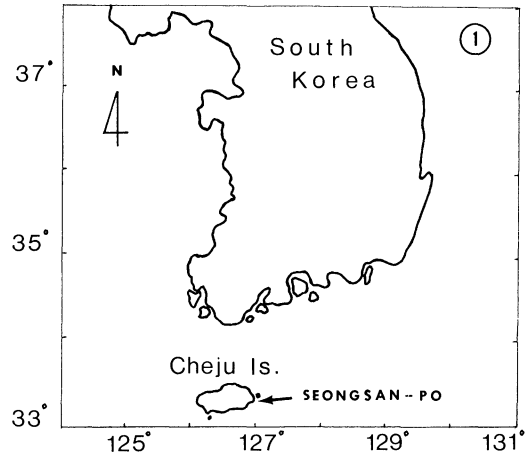


FIG. 1. Map showing collection site.

tetrasporangiorum lanceolata pedicellata in ramis determinatis monosiphonibus evolutantia; tetrasporangia sphaerica tetraedrice divisa, cellulis tegentibus sterilibus incomplete tecta; rami spermatangiorum lanceolati pedicellati in ramis determinatis monosiphonibus evolutantes; spermatangia elliptica aliquot in cellula parentali; procarpia cum duo turmis sterilibus alterna in successivis segmentis polysiphonibus ramulorum brevium specialite evolutorum, e cellula pericentrali secunda vel tertia oriunda; cystocarpia sphaerica vel obovata ostiolata; carposporangia sphaerica. Plantae cum historia vita simili *Polysiphoniae.*

Frond erect, sympodial in growth, forming an indeterminate or determinate branch from every segment of main axes in bilateral-dorsiventral manner, attached by rhizoidal holdfast; lightly corticated main axes polysiphonous, cutting off 5 pericentral cells alternately from central cells; indeterminate branches producing a few orders of lateral branches in the same pattern as main axes, polysiphonous with 5 pericentral cells; determinate branches monosiphonous, dividing 1–3 times by sympodial growth, modified into hair-like filaments in older thalli and fertile female branchlets; lanceolate pedicellate tetrasporangial stichidia developing on monosiphonous determinate branches; several elliptical spermatangia on each parent cell; procarps with two sterile groups alternate on successive segments of specially developed short polysiphonous branchlets, derived from the second or third pericentral cell; spherical to obovate cystocarps ostiolate; carposporangia spherical. Plants with *Polysiphonia*-type life history.

Dasysiphonia chejuensis Lee and West, sp. nov.

Frons pro generis descriptione, rosea-rubra, mollis, 3–5 cm alta in culturis; axes principales torti leviter, 130–230 μm diam.; cellulae pericentrales raro semel transverse divisae, 200–400 μm longae; stichidia tetrasporangiorum cum pedicellis unicellulosis, 100–130 μm lata, 700–800 μm longa; tetrasporangia 35–40 μm diam.; rami spermatangiorum

cum pedicellis unis vel multicellularis, 40–60 μm lati, 200–300 μm longi; spermatangia 3–5 in cellula parentali, 2.5–3.5 μm lata, 4–6 μm longa; procarpia cum turmis sterilibus bicellularibus primibus et unicellularibus secundariis; rami carpogoniales 4-cellulares; cystocarpia 580–650 μm lata, 600–680 μm alta; carposporangia 20–22 μm diam.

Frond as described for the genus, pink-red, soft, 3–5 cm high in culture; main axes slightly twisted, 130–230 μm diam.; pericentral cells rarely divided once transversely, 200–400 μm long; tetrasporangial stichidia with unicellular pedicels, 100–130 μm broad, 700–800 μm long; tetrasporangia 35–40 μm diam.; spermatangial branches with uni- or multicellular pedicels, 40–60 μm broad, 200–300 μm long; spermatangia 3–5 on each parent cell, 2.5–3.5 μm broad, 4–6 μm long; procarps with 2-celled first and 1-celled second sterile groups; carpogonial branches 4-celled; cystocarps 580–650 μm broad, 600–680 μm high; carposporangia 20–22 μm diam.

Type locality: KOREA. Seongsan-po, Cheju Island.

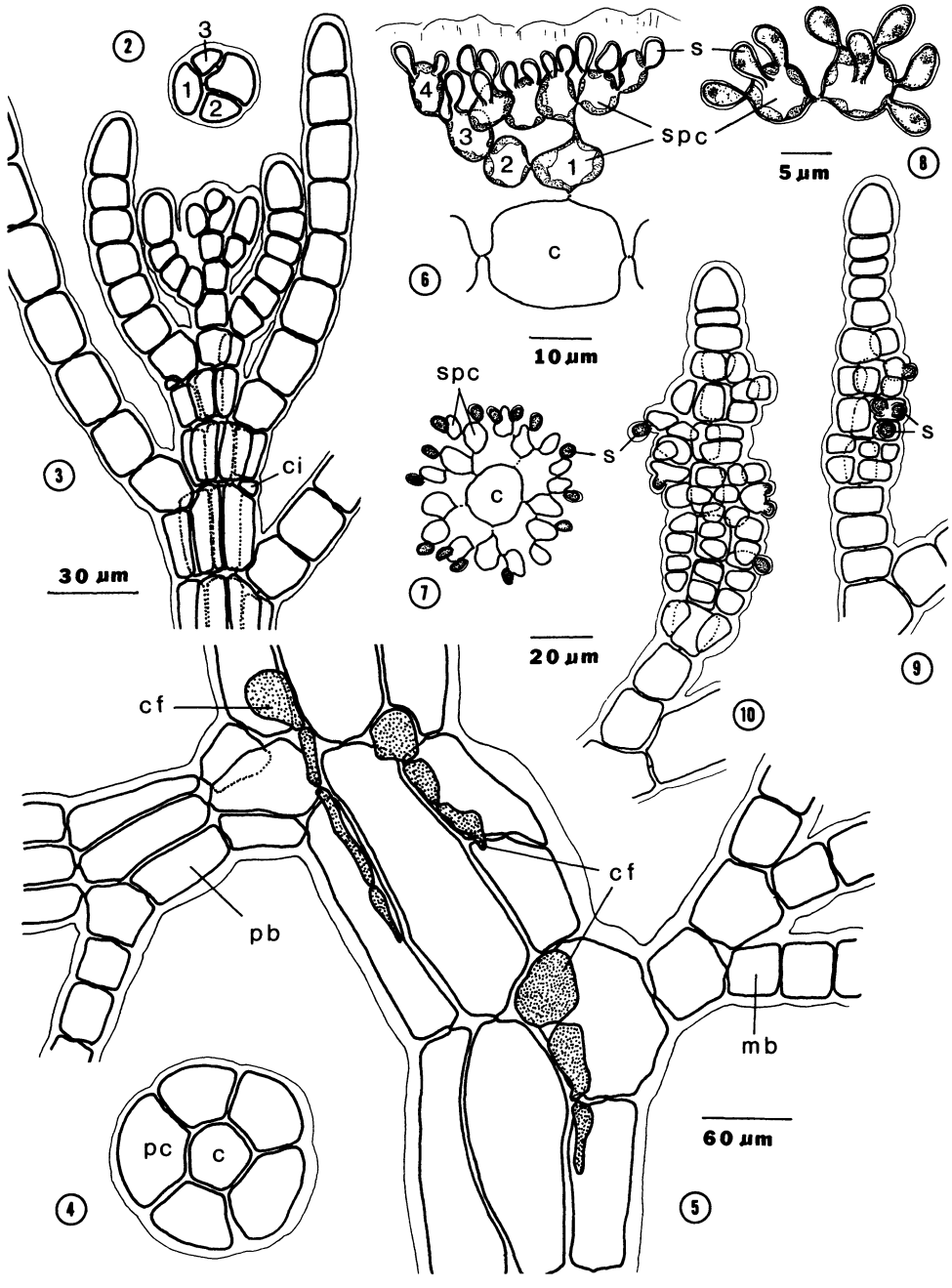
Holotype: UC 1446018 Cystocarpic plant (pressed 18 October 1978) derived from tetraspore germlings after two months of culture. Isotype: UC 1446019 Male plant (same as holotype). UC 1446020 Tetrasporangiate plant (pressed 18 October 1978) derived after three months of culture from vegetative shoot apex of tetrasporophyte collected 5 July 1978 from the type locality. This tetrasporophyte produced spores which developed into the ♀ holotype and ♂ isotype plants.

MATERIALS AND METHODS

Both procarpic and tetrasporangiate plants were collected from Seongsan-po, Cheju Island, Korea (Fig. 1), 5 Jul 1978 at shady rock recesses in the upper subtidal zone. They were 2–3 cm high, bearing mature tetrasporangial stichidia or procarps. Surface water temperature at the time of collection was 20°C. The plants were placed in sea water and transferred in a cooler to Seoul National University where they were held at 22–25°C for 7 days prior to air shipment to Berkeley, California. Excised vegetative apices of both tetrasporangiate and procarpic thalli were isolated into unialgal culture in ½ strength PES medium (McLachlan, 1973) under 15–17°C, 300–800 lux cool white fluorescent light, 14:$\overline{10}$ LD. Later, some of the isolates were removed to 15°C, 800–1500 lux, 16:$\overline{8}$ LD.

OBSERVATIONS

Vegetative Structure.—As the subapical cell cuts off a new apical cell obliquely and alternately from the upper corner in every segment, the thallus shows typical sympodial growth. The branches extend bilaterally, displaying a dorsiventral character (Fig. 3) sensu Falkenberg (1901) and Parsons (1975). Generally the fourth to sixth axial cell from the apex begins to cut off pericentral cells. The first pericentral cell always is formed below the lateral branch of the same segment, and the second is cut off at either the left or right side of the first, while the third develops opposite the second (Fig. 2). The fourth and fifth pericentral



FIGS. 2–10. Vegetative structures and spermatangium formation. 2. Transverse view of pericentral cell formation in apex, numbers indicating developmental order. 3. Apex showing sympodial growth. 4. Transverse view of polysiphonous axis with five pericentral cells. 5. Part of main axis with cortical filaments, polysiphonous indeterminate (left) and monosiphonous determinate (right) branches. 6. Mature spermatangia in longitudinal

cells also are formed alternately so that five pericentral cells constantly develop in the main axes and in all polysiphonous lateral branches (Fig. 4).

Monosiphonous determinate branches (or pseudolaterals) originate from old apical cells and generally grow dichotomously to 0.5–1.0 mm in length. Polysiphonous branches take the place of monosiphonous branches, each bearing a short basal segment and a typical apex. They produce monosiphonous laterals from every segment except the basal one (Fig. 5).

Cortical cells often arise from the basal end of the first pericentral cell (Fig. 3), and also from other pericentral cells later. They develop into cortical filaments that grow downward between pericentral cells of the subjacent segments (Fig. 5). Prostrate stoloniferous branches develop from the holdfast and attach to the substrate, producing erect fronds at irregular intervals.

Tetrasporangial Stichidia.—Tetrasporangial stichidia develop adaxially on monosiphonous determinate branches and are clearly distinguishable as short linear cells (Figs. 12, 13). Fertile segments of young stichidia develop five pericentral cells alternately, each of which divides transversely into a tetrasporangial initial above and a stalk cell below (Figs. 11a,b, 13, 14). Then the stalk cell cuts off a cell outward, which divides anticlinally into two or three cover cells (Figs. 11c, 15, 18, 19). Sometimes, these cover cells are divided transversely again (Fig. 11d). Such cells, however, usually do not cover tetrasporangia completely. Tetrasporangia mature acropetally in a stichidium, and the stalk cell and cover cells remain unpigmented (Figs. 16, 17). Mature stichidia are lanceolate, 100–130 μm broad and 700–800 μm long, and consist of about 20 fertile segments and a sterile terminal cell. Rarely, the pedicel may become polysiphonous, and stichidia may branch. Tetrasporangia are spherical and 35–40 μm in diameter.

Spermatangial Branches.—Spermatangial branches also develop on monosiphonous determinate branches as do tetrasporangial stichidia (Figs. 9, 10). Each spermatangial branch first cuts off alternately five pericentral cells that become primary spermatangial parent cells. They cut off a few secondary parent cells first transversely and then anticlinally. A few tertiary and quaternary parent cells are also cut off in turn, so that these parent cells are seriate on the central cell (Figs. 6, 7). Each sper-

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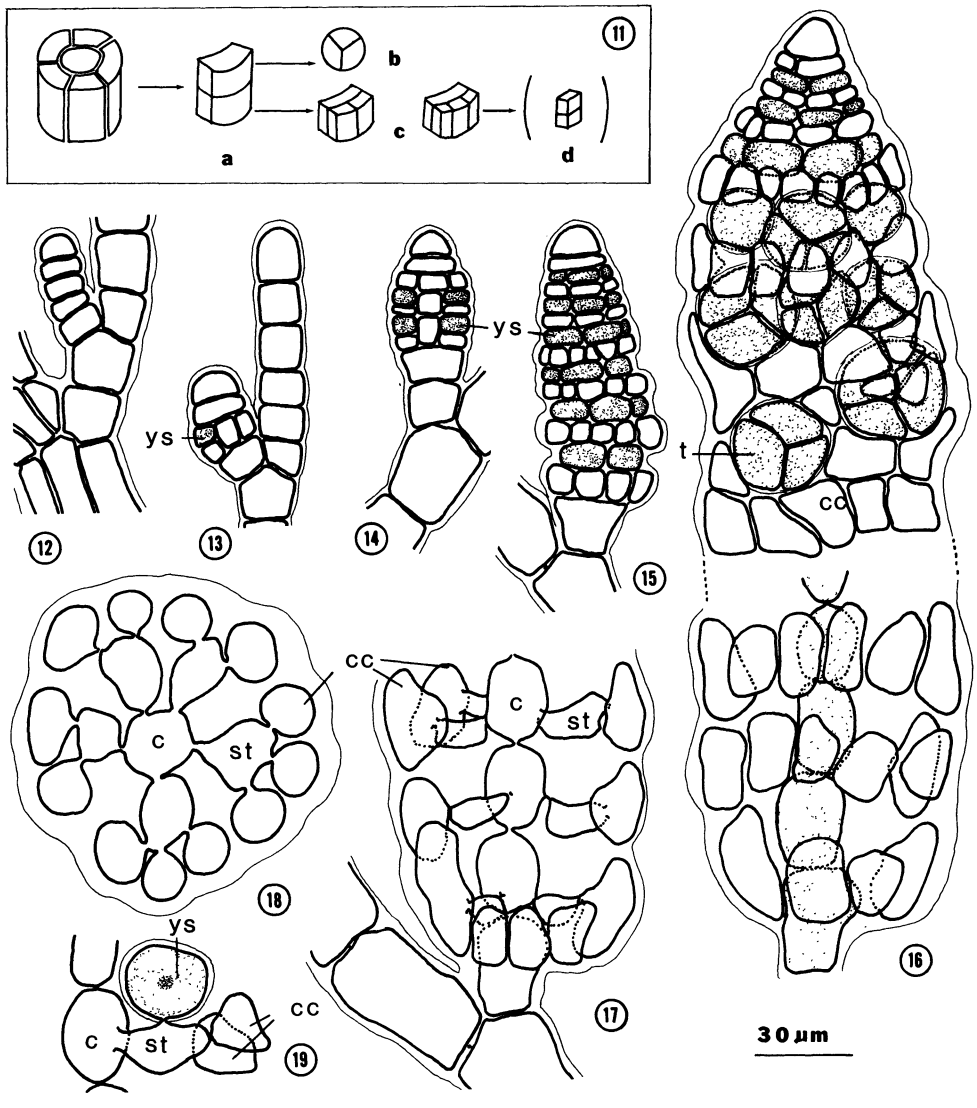
section of fertile branch, showing seriate spermatangial parent cells. Numbers indicate developmental order. 7. The same as Fig. 6, cross section. 8. Two spermatangial parent cells with three to five spermatangia. 9,10. Development of spermatangia in monosiphonous branches. (c: central cell, cf: cortical filament, ci: cortical cell initial, mb: monosiphonous determinate branch, pb: polysiphonous indeterminate branch, pc: pericentral cell, s: spermatangium, spc: spermatangial parent cell).



FIGS. 11–19. Tetrasporangium formation. 11. Diagrammatic illustration of tetrasporangium and cover cell formations: a, pericentral cell dividing anticlinally; b, tetrasporangium; c, stalk cell and superficial cell by periclinal division, with superficial cell dividing longitudinally into two or three cover cells; d, cover cell sometimes dividing anticlinally into two cells. 12–15. Development of tetrasporangial stichidia. 16. Mature stichidium. 17. Lower part of empty stichidium. 18. Transverse view of empty stichidium. 19. Young sporangium in longitudinal view. (c: central cell, cc: cover cell, st: stalk cell of sporangium, t: tetrasporangium, ys: young sporangium).

matangial parent cell produces three to five spermatangia (Fig. 8). Some primary and secondary parent cells may remain without development of spermatangia (Fig. 6). Only the parent cells are pigmented. Mature spermatangial branches are lanceolate and may rarely divide once in the middle to lower portion. They are 40–60 μm broad, 200–300 μm long, and consist of about 20 fertile segments up to the terminal cell. Spermatangia are elliptical, 2.5–3.5 μm broad and 4–6 μm long.

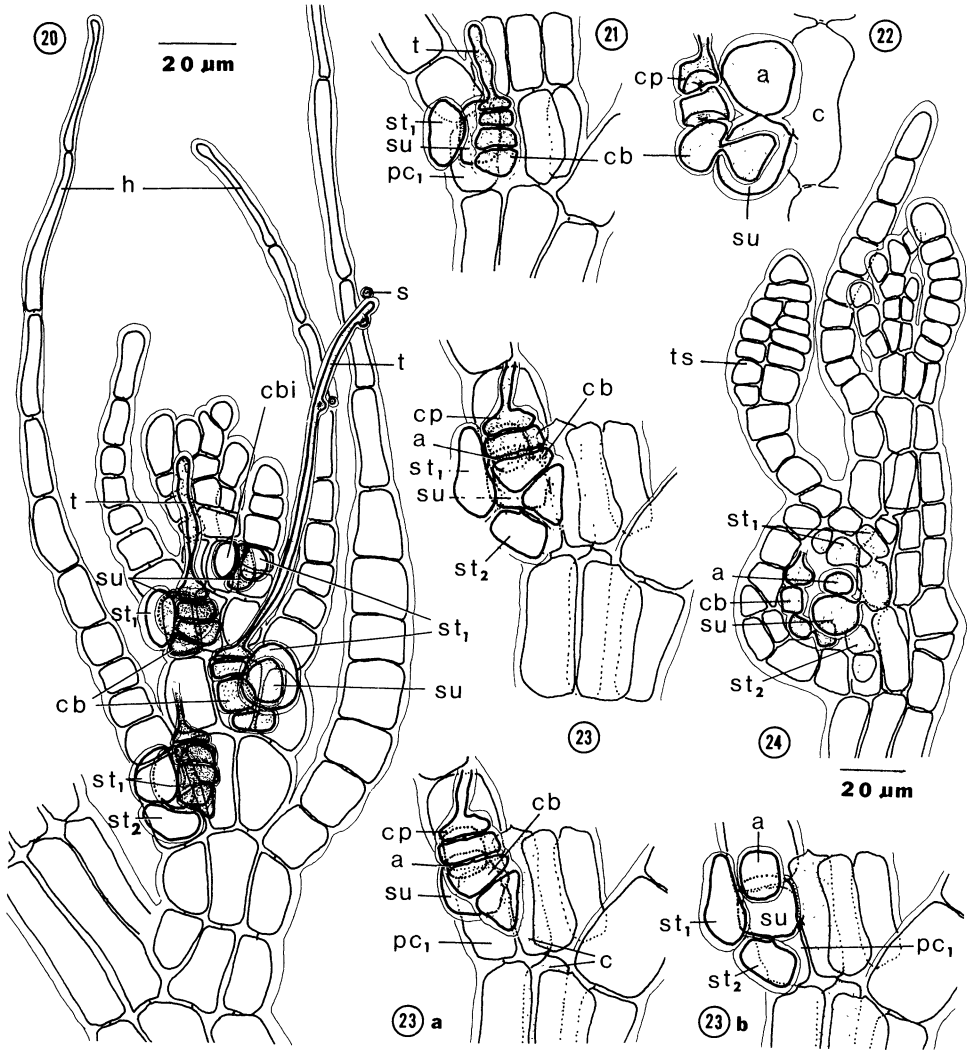
Female Reproductive System.—Female reproductive structures occur on specially developed 200–600 μm long polysiphonous branchlets in mid- to upper portions of main axes and polysiphonous laterals. Fertile branchlets characteristically bear monosiphonous determinate branches with long hair-like terminal portions (Fig. 20).

Procarps develop on the third segment from the base of the fertile branchlet, and are formed successively in an alternate manner on every segment throughout the polysiphonous portion. The second or third pericentral cell located adjacent to the first becomes the supporting cell (Figs. 21, 23a,b). It cuts off a first sterile cell, and then an initial cell of the carpogonial branch. The carpogonial branch is always abaxial to the central axis (Figs. 20, 21, 23). After development of the carpogonial branch, the supporting cell cuts off a second sterile cell below the first (Figs. 23, 23a). The first sterile cell divides anticlinally into two cells whereas the second sterile cell remains undivided (Fig. 20, lower procarp). The carpogonial branch consists of four cells. The first cell of the branch is derived from the lower part of the supporting cell, and the others extend up over the supporting cell (Fig. 21). The trichogyne is quite elongate. Procarps develop no pericarp initials before fertilization.

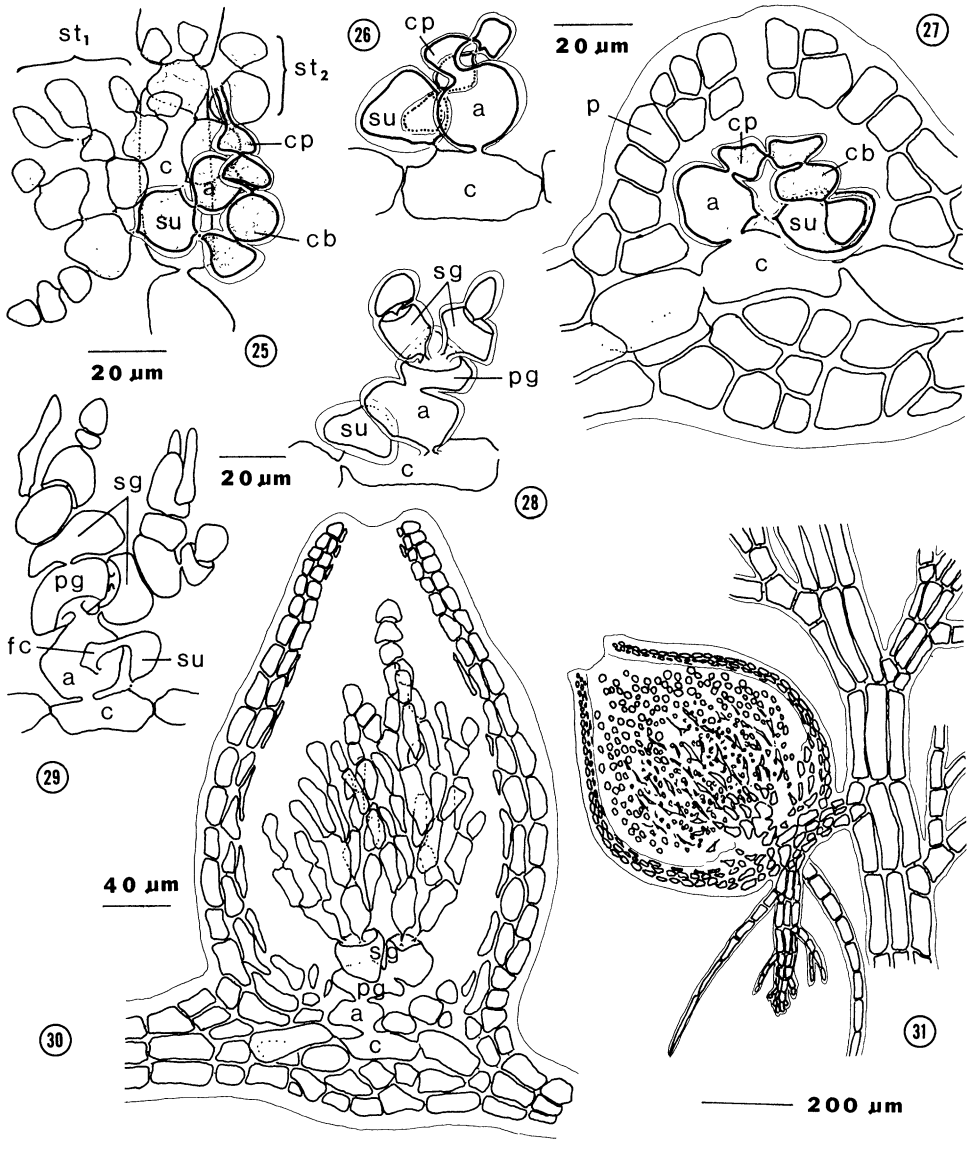
After fertilization, the supporting cell cuts off an auxiliary cell upward near the carpogonium (Figs. 22, 23b). The carpogonium fuses directly to the auxiliary cell before the carpogonial branch forms a fusion cell. Then the auxiliary cell fuses with the central cell (Figs. 26, 27). Later, the supporting cell and the fusion cell of the carpogonial branch form a single irregular fusion cell (Fig. 29).

The primary gonimoblast cell is derived from the distal end of the auxiliary cell, and gives rise obliquely to two secondary gonimoblast cells (Fig. 28). Subsequently they form a large Y-shaped fusion cell in the basal portion of the cystocarp (Fig. 30). Additional oblong gonimoblast cells arise from this fusion cell and produce carposporangia terminally and laterally.

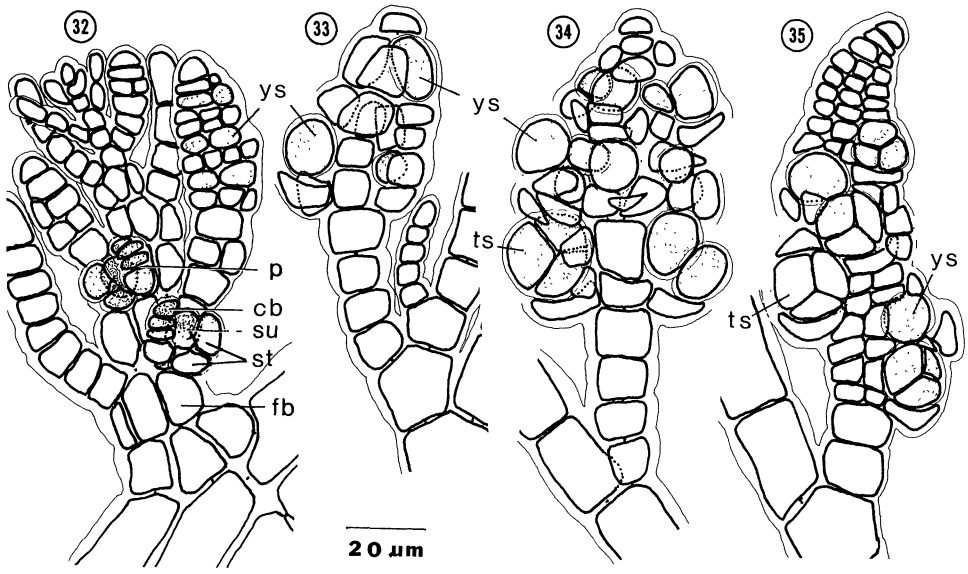
Sterile cells in a fertilized procarp divide radially (Figs. 24, 25), and occupy the basal portion of the young cystocarp, whereas three central cells in the fertile portion (the one connected with the auxiliary cell and the two adjacent to this central cell) enlarge more, cutting off some "nutrient" cells. The pericarp is formed through successive divisions of pericentral cells around the procarp after fertilization (Figs. 24, 27). In a



FIGS. 20–24. Development of female reproductive structures. 20. Fertile female branchlet with procarps. 21. Procarp with young carpogonial branch. 22. Carpogonial branch and auxiliary cell on supporting cell. 23. Two sterile cells, carpogonial branch and auxiliary cell on supporting cell. a, b. Dissected view of Fig. 23: a, carpogonial branch, auxiliary cell and supporting cell adjacent to the first pericentral cell; b, sterile cells, auxiliary cell and supporting cell adjacent to the first pericentral cell. 24. Part of female fertile branch, showing early post-fertilization process and development of tetrasporangial stichidium at the same time. (a: auxiliary cell, c: central cell, cb: carpogonial branch, cbi: carpogonial branch initial, cp: carpogonium, h: hair-like modification of monosiphonous branch, pc_1: first pericentral cell, s: spermatium, st_1: first sterile cell, st_2: second sterile cell, su: supporting cell, t: trichogyne, ts: tetrasporangial stichidium).



FIGS. 25–31. Development of female reproductive structures. 25. Development of additional sterile cells after fertilization. 26. Fusion between carpogonium and auxiliary cell, auxiliary cell also fusing to central cell. 27. The same as Fig. 26, showing early pericarp formation. 28. Development of young gonimoblast cells from auxiliary cell. 29. Development of gonimoblast cells, with carpogonial branch and supporting cell forming fusion cell. 30. Young cystocarp. 31. Mature cystocarp. (a: auxiliary cell, c: central cell, cb: carpogonial branch, cp: carpogonium, fc: fusion cell of carpogonial branch, p: pericarp, pg: primary gonimoblast cell, sg: secondary gonimoblast cell, st_1: first sterile group, st_2: second sterile group, su: supporting cell).



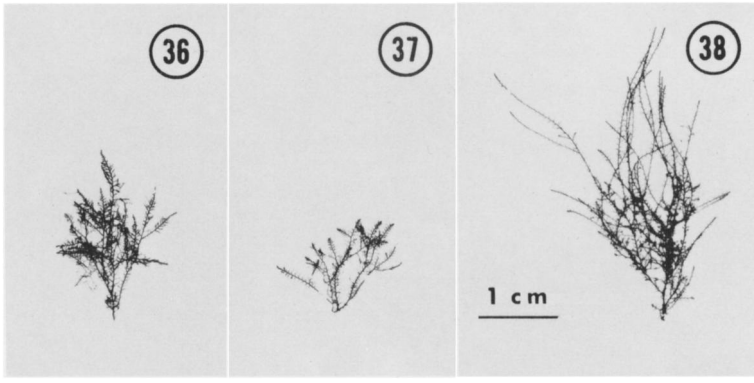
FIGS. 32–35. Tetrasporangium formation on female thallus. 32. Fertile female branch with procarps and young tetrasporangial stichidia. 33–35. Development of tetrasporangial stichidia in female thalli. (cb: carpogonial branch, fb: fertile female branchlet, p: procarp, st: sterile cells, su: supporting cell, ts: tetrasporangium, ys: young sporangium).

fully mature pericarp there are two to three cell layers and an ostiole at the top (Figs. 30, 31).

Tetraspores cultured from the original field-collected tetrasporophyte become either male of female gametophytes, which show the same morphological characters as field-collected plants (Figs. 36–38). Both field and laboratory-cultured female thalli produce viable carpospores when they are crossed with male plants. Carpospores grow into normal tetrasporophytes. Under certain culture conditions, however, female plants form tetrasporangial stichidia together with cystocarps, or stichidia alone (Lee & West, unpublished data). Such stichidia on female thalli are fundamentally similar in appearance to those on tetrasporophytes, except for a slightly irregular shape because sporangia do not mature in an acropetal order (Figs. 24, 32–35).

DISCUSSION

In general, descriptions of new taxa of macroscopic marine algae are based exclusively on field-collected specimens rather than plants cultured in the laboratory. Our description thus represents a departure from conventional procedures. Very few new species have been cultured, and if cultured, they generally do not show a complete life history, or morphological and reproductive characters differ in cultured compared to field-



FIGS. 36–38. Herbarium specimens. 36. Holotype cystocarpic plant (UC 1446018) derived from tetraspore of isotype tetrasporangiate plant. 37. Isotype male plant (UC 1446019) obtained in same way as holotype. 38. Isotype tetrasporangiate plant (UC 1446020) collected from type locality.

collected material. Our cultured plants, however, are virtually identical in morphology to the plants collected in the field.

According to Falkenberg (1901), Rosenberg (1933) and Parsons (1975), the Dasyaceae is characterized by sympodial growth of the apices; monosiphonous and polysiphonous branches develop radially or bilaterally-dorsiventrally; tetrasporangia verticillate in stichidia; procarps consist of a first sterile group; carpogonial branch and second sterile group develop sequentially from the supporting cell; and an auxiliary cell fuses with the central cell. According to these criteria *Dasysiphonia* clearly belongs in the Dasyaceae.

Among genera of the family, *Dasya, Dasyopsis* and *Rhodoptilum* Kylin are closely related with respect to tetrasporangial and procarpial characters, whereas *Heterosiphonia, Thuretia* Decaisne and *Colacodasya* Schmitz are related in tetrasporangium formation and apical structure (Parsons, 1975). *Dictyurus* Bory is a distinct genus by virtue of the reticulate thallus (Svedelius & Nygren, 1946). The other genera are characterized as follows: *Dasyella* Falkenberg by transversely divided pericentral cells (Falkenberg, 1901), *Pogonophorella* Silva by dichotomous branches arranged radially and pericentral cells obscured by cortical filaments (Kylin, 1941), *Amphisbetema* Weber-van Bosse by a sympodial dichotomous main axis and monopodial branches (Weber-van Bosse, 1913), and finally *Tapeinodasya* Weber-van Bosse by bilateral and dorsiventral prostrate branches as well as radial erect branches (Weber-van Bosse, 1904).

Rhododictyon, described and tentatively placed in the Dasyaceae by Taylor (1961), was transferred by Schneider (1975) to the Ceramiaceae because of tetrasporangial placement, a decision supported by van den Hoek (1978). *Heterodasya* Joly et de Oliveira (1966) was provisionally transferred to the Rhodomelaceae by Parsons (1975) on the basis of the

TABLE 1. A comparison of some taxonomic characters of *Dasysiphonia* with two related genera of Dasyaceae.

Characters	Genera		
	*Dasya**	*Heterosiphonia**	*Dasysiphonia*
Vegetative structures			
Branching	radial	bilateral/dorsiventral	bilateral/dorsiventral
Pericentral cells & sequence of formation	5(4), circular	4–12, alternate	5, alternate
Tetrasporangial stichidia			
Pericentral cells	5–7	5–7	5
Presporangial cover cells**	–	+	–
Envelopment by cover cells	partially	completely	partially
Spermatangial branches			
Pericentral cells & sequence of formation	4, alternate	4–5, alternate	5, alternate
Female reproductive structures			
Site of formation	polysiphonous branch	monosiphonous branch	polysiphonous special branchlet
Pericentral cells & sequence of formation	5, circular	5, alternate	5, alternate
Procarp position on axis	spiral	irregular	alternate
Location of supporting cell	3rd pericentral cell	last pericentral cell	2nd or 3rd pericentral cell
Pericarp initials before fertilization	–	+	–
Connecting cell	±	±	–

* Referred to by Falkenberg (1901), Rosenberg (1933) and Parsons (1975).
** Cover cells cut off from sporangial initial cell (Parsons, 1975).

monopodial axis, stichidia with branched laterals (trichoblasts) and 1–3 sporangia borne per segment.

On the other hand, *Dasysiphonia* is characterized by 1) sympodial bilateral-dorsiventral branches, 2) five pericentral cells derived alternately from the central cell, 3) lightly corticated main axes without adventitious branches, 4) spermatangial branches and tetrasporangial stichidia alternately developing five pericentral cells and forming on monosiphonous branches, 5) tetrasporangia incompletely covered by cover cells, 6) procarps occurring alternately in successive segments on specially developed short polysiphonous branchlets, and 7) second or third pericentral cell adjacent to the first becoming the supporting cell. Pericarp initials are not seen before fertilization. A connecting cell is not formed from the carpogonium. The auxiliary cell fuses directly with the central cell.

Dasysiphonia shows some relation to *Heterosiphonia, Thuretia* and *Colacodasya* in bilateral-dorsiventral branches and alternately developing pericentral cells. However, *Heterosiphonia* differs reproductively from *Dasysiphonia* as mentioned in Table 1, *Thuretia* differs in heavy cortication that obscures the pericentral cells and also in tetrasporangia being completely surrounded by cover-cells (Parsons, 1975), and *Colacodasya* differs in its parasitic character (Falkenberg, 1901; Hollenberg, 1970).

Reproductively, *Dasysiphonia* shows close affinity to *Dasya, Dasyopsis* and *Rhodoptilum,* in which tetrasporangia are surrounded only partially by cover-cells. However, *Dasya* is distinguished from *Dasysiphonia* by the following basic characters: 1) radially arranged branches, 2) circularly developing pericentral cells, and 3) the supporting cell cut off from the third pericentral cell opposite the first (Rosenberg, 1933; Parsons, 1975). In *Dasyopsis* and *Rhodoptilum* the main axes are heavily corticated, obscuring pericentral cells (Falkenberg, 1901; Rosenberg, 1933; Kylin, 1956). The latter genus also shows strongly compressed axes (Abbott & Hollenberg, 1976).

The life histories of *Heterosiphonia* and *Dasya* were investigated in culture by West (1970) and Parsons (1975). Parsons indicated that *D. clavigera* showed a typical *Polysiphonia*-type life history, whereas West demonstrated that *H. japonica* (as *H. densiuscula* and *H. asymmetria*) is obligately apomeiotic. In addition mixed phase reproduction (see van der Meer & Todd, 1977, regarding the term "mixed phase"), male/tetrasporangia, female/tetrasporangia, or male/female on a single thallus is reported from field and culture studies of various genera in the Ceramiales, e.g., *Antithamnion, Polysiphonia* and *Callithamnion,* etc. (West & Norris, 1966; Edelstein & McLachlan, 1967; Knaggs, 1969; Rueness & Rueness, 1973; Whittick & West, 1979).

According to our experiment, *Dasysiphonia chejuensis* shows basically a typical *Polysiphonia*-type life history. However, in culture it shows additionally a female/tetrasporangia mixed reproductive system. Cytological characters as well as factors inducing mixed phase reproduction are now under investigation.

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