

MORPHOLOGICAL STUDIES ON SOME TROPICAL SPECIES OF  
*GRACILARIA* GREV. (GRACILARIACEAE, RHODOPHYTA):  
TAXONOMIC CONCEPTS BASED ON REPRODUCTIVE MORPHOLOGY

Suzanne Fredericq and James N. Norris

**Abstract**

Taxonomic features used to distinguish selected *Gracilaria* species from the tropical-subtropical Western Atlantic were investigated. Two groups are recognized based upon reproductive morphological differences shown by the female reproductive structures, and differences in the origin of spermatangial conceptacles and tetrasporangia. *Group 1* consists of *G. debilis* (Forsskål) Børgesen and *G. crassissima* P. et H. Crouan; *Group 2* of *G. tikvahiae* McLachlan and *G. cervicornis* (Turner) J. Agardh. *Group 1* is distinguished by the following features: the gonimoblast does not originate directly from the fusion cell; the direction of cystocarp development occurs principally horizontally; the number and shape of the pericarp layers is fixed prior to the formation of the fusion cell; the cystocarp cavity is present prior to the appearance of gonimoblast initials; the fusion cell becomes highly ramified and not distinguishable; the gonimoblast originates early in development from inner pericarp cells connected to the fusion cell; absorbing filaments connecting gonimoblast and upper pericarp are absent, but basal connections are formed between the inner pericarp and placenta; spermatangia originate from cortical, subcortical, or medullary cells; the tetrasporangia originate either basally or laterally from cortical cells. In contrast, *Group 2* is characterized by: a gonimoblast that originates directly from the fusion cell; the direction of the cystocarp development occurs principally vertically; the pericarp is formed concomitantly with the formation and expansion of the fusion cell; the cystocarp cavity is formed after the appearance of gonimoblast initials; the fusion cell is prominent and solid; the gonimoblast develops late and originates from cells cut off from the fusion cell; absorbing filaments are present that only connect the gonimoblast and upper pericarp; spermatangia originate only from cortical cells; the tetrasporangia originate only basally from cortical cells. These two groups are suggested to form the basis of two distinct genera.

**Introduction: Historical Review of Reproductive Structures**

Members of the genus *Gracilaria* Grev. (Greville 1830, p. lvi), *nomen conserv.* (Gigartinales Schmitz, Gracilariaceae Nägeli, *vide* Silva 1980, p. 83) are widespread from sub-boreal to tropical waters. The taxonomy of this economically important agar-producing genus is confused by the high degree of morphological and anatomical variation exhibited within species (e.g., Chapman et al. 1977), which has complicated recognition of species. As Dawson (1949) noted, although *Gracilaria* is a very polymorphic genus vegetatively, it has remarkably constant reproductive structures. Species limits are ill-defined and the genus is in need of major revision (e.g., Papenfuss 1953, 1967; Bird and McLachlan 1982, 1984).

Taxonomic and floristic treatments of *Gracilaria* in the tropical-subtropical Western Atlantic are by Taylor (1960, 1969) and Oliveira et al. (1983), and regionally from Puerto Rico (Diaz-Piferrer and Caballer de Perez 1964; Ortiz Sotomayor 1976; Ortiz Sotomayor and Almodovar 1982; Véléz Villamil 1981), and the northwestern Atlantic (McLachlan 1979).

Recent studies from other areas that involve reproductive morphology in *Gracilaria* have been undertaken by Bodard (1964, 1967), Chang and Xia (1964, 1976); Oliveira (1969); Oza (1976); Kraft (1977); Yamamoto (1978); Edelstein et al. (1978); Yang and Chiang (1982); Delivopoulos and Tsekos (1983); Abbott (1983); Bird and McLachlan (1984); and Hoyle (1984). Ecological studies on *Gracilaria* reproduction are few. The only studies of reproductive seasonality of tropical species of *Gracilaria* are those of Umamaheswara Rao (1973), Hoyle (1978), Trono and Azanza-Corrales (1981), and Hay and Norris (1984). Hay and

Norris (1984) found six sympatric species of Caribbean Panama *Gracilaria* to be fertile throughout the year, with no spatial or temporal isolation of reproduction, and suggested chemical or structural differences may be important in preventing hybridization.

Sjöstedt (1926) was the first to recognize carpogonial branches in *Gracilaria*. His interpretation of those structures was confirmed by Dawson (1949). The carpogonial branch develops from a transformed cortical cell that functions as the primordium (see Sjöstedt 1926; Yamamoto 1978). The primordium cuts off a supporting cell and an apical cell. This apical cell divides transversely forming a two-celled carpogonial branch, the lower cell becoming the hypogynous cell and the upper cell becoming the carpogonium bearing the trichogyne (see Sjöstedt 1926; Yamamoto 1978). Before development of the carpogonial branch is completed, the supporting cell also cuts off one or two cells which retain their vegetative character as sterile lateral branches (Sjöstedt 1926; Yamamoto 1978). Johnson (1888) commented on the presence of carpogonial branches originating after pericarp formation in *G. verrucosa* (Huds.) Papenfuss [as *G. confervoides* (L.) Grev.]; however, Sjöstedt (1926) felt Johnson's study was "fragmentary and in part inaccurate."

In describing the Gracilariaceae, Kylin (1930) noted that the family is distinguished by the occurrence of a large irregular fusion cell from which the gonimoblast develops after enlargement of the fertilized carpogonium and its fusion with several neighboring cells. Several interpretations exist regarding presence or absence of an auxiliary cell in *Gracilaria*. Sjöstedt (1926), later corroborated by Oliveira (1969), assumed that *Gracilaria* never shows an auxiliary cell and considered the carpogonium to be the starting point for the fusion cell. Sjöstedt further stated that the function of the auxiliary cell is taken over by the multinucleate basal cells of the sterile branches and that none of these cells becomes the typical auxiliary cell detectable before fertilization, with the carpogonium not degenerating after fertilization. More recently, Oza (1976) reported that in *G. corticata* J. Ag. an auxiliary cell is absent, and the fertilized carpogonium fuses with the hypogynous cell, the supporting cell, and the surrounding sterile cells. In studying *G. tikvahiae* McLachlan, Edelstein et al. (1978, as *G. species*) could not detect connections between the carpogonium, the hypogynous cell, and the supporting cell, but noted that the latter two cells increase in size while the carpogonium shrivels. They regarded further fusion to result in a single large cell which became irregularly shaped and strongly lobed as the fusion progressed. In contrast, Greig-Smith (1954) reported that the carpogonium in *G. foliifera* (Forsskål) Borg. (as *G. multipartita* J. Ag.) develops a short filament that connects to the auxiliary cell. This auxiliary cell is borne directly on the supporting cell and later develops the fusion cell. (If this is the case, it suggests that it does not belong in the Gigartinales.)

In a more detailed account Yamamoto (1978) described for Japanese *Gracilaria* species a connecting tube that emerges from the inflated basal portion of the carpogonium after fertilization. The connecting tube then makes a connection with the basal cell of a sterile branch. Assuming that the diploid nucleus in the carpogonium entered the basal cell, he considered it to be the auxiliary cell. After completion of the ephemeral connection between carpogonium and auxiliary cell, the carpogonium finally degenerates (Yamamoto 1978). Occasionally the pit-connection between the carpogonium and the hypogynous cell gradually widens, allowing the diploid nucleus to move into the hypogynous cell. In this case, it is the hypogynous cell that forms a connection with the auxiliary cell (Yamamoto 1978). The auxiliary cell then unites with a neighboring cortical cell and with the supporting cell through a wide pit-connection. In this case, the auxiliary cell serves as the starting point of a big

fusion cell, which involves the hypogynous and supporting cells and eventually produces the gonimoblast at its periphery (Yamamoto 1978).

In summary, three sites of origin for the fusion cell have been proposed: (1) a typical auxiliary cell (Greig-Smith 1954; Yamamoto 1978), (2) the carpogonium (Sjöstedt 1926; Kylin 1930; Oliveira 1969), and (3) fusion among the hypogynous, supporting, and neighboring cells (Yamamoto, 1978).

Thuret and Bornet (1878) illustrated elongated, concentric cells within the cystocarp, which they thought originated either from the pericarp or from the gonimoblast. Sjöstedt (1926) suggested a nutritive function for those cells, naming them "nutrient tubular cells," capable of taking nutrients from the cortical cells and transferring them to the gonimoblast parenchyma. Dawson (1949) coined the term "nutritive filaments," which was subsequently accepted by Børjesen (1950) and Ohmi (1958). Sjöstedt (1926), later corroborated by Dawson (1949), described two kinds of cystocarps in *Gracilaria*. One type was based on the absence of nutritive filaments and the presence of a gonimoblast parenchyma which consists of a highly nutritive-rich multicellular tissue of small cells. The other type was based on the presence of nutritive filaments with a gonimoblast parenchyma of relatively few, though larger, and comparatively nutritive-poor elongated cells. Ohmi (1958a) further correlated a broad-based gonimoblast parenchyma with the presence of nutritive filaments and a small-based one with the absence of those filaments. Dawson (1949) recognized two genera on these features. Based on the cystocarps without nutritive filaments, he described a new genus, *Gracilariopsis* Dawson [generic type: *Gracilariopsis sjoestedtii* (Kylin) Dawson], segregating it from *Gracilaria* Grev., which had cystocarps with nutritive filaments.

Oliveira (1969) mentioned that occasionally in *Gracilaria verrucosa* (Huds.) Papenfuss he was unable to observe "nutritive filaments," suggesting that the filaments may not possess any systematic value. Earlier, Bodard (1967) had also considered the use of this character for generic separation to be weak. Both authors were apparently unaware that Papenfuss (1967) had reduced the genus *Gracilariopsis* Dawson to taxonomic synonymy with *Gracilaria* Grev. after having examined the British material of *Gracilaria verrucosa* (Huds.) Papenfuss [lectotype: *G. confervoides* (L.) Grev.]. He reported that the presence of nutritive or "connecting" filaments could not always be confirmed, and that the size of the placental cells did not differ fundamentally from the ones of *G. sjoestedtii*.

Yamamoto (1975, 1978) tentatively used the term "nutritive filaments" awaiting a better understanding of their function. Kraft (1977) preferred the use of a purely neutral descriptive term and suggested "traversing filaments." Børjesen (1950) noted that with large and vacuolated gonimoblast cells, typical for some *Gracilaria*, connecting filaments penetrate the gonimoblast tissue from below in *G. millardetii* (Mont.) J. Ag. Umamaheswara Rao (1972) observed the same phenomenon in some Indian species of *Gracilaria*. Yamamoto (1975) regarded the "nutritive filaments" as subsidiary in any systematic treatment of the genus. In order to use a consistent, uniform terminology, we will refer to "nutritive," "connecting," or "traversing" filaments as "absorbing" filaments throughout this study (and this volume) as used by Mikami (1965) and Abbott (1972).

Dawson (1949) first demonstrated the taxonomic importance of the shape and origin of spermatangial conceptacles. Ohmi (1958a), in his monograph on Japanese *Gracilaria* species, stressed that they were the most important characters to distinguish species. Later, Yamamoto (1975) divided the genus into three subgenera based on the three different types of male organs: (1) *Gracilariella*—with superficial spermatangia, scattered continuously over the thallus surface, e.g., *G. chorda* Holmes; (2) *Textoriella*—with spermatangia in

shallowly depressed concave conceptacles in the cortex, with each spermatangial mother cell primordium forming a branch system covering the floor of the conceptacle at maturity, e.g., *G. textorii* (Sur.) DeToni; and (3) *Gracilaria*—with spermatangia in deep cup-shaped conceptacles within the cortex, with each spermatangial mother cell primordium forming a branch system covering the entire inner surface of the conceptacle at maturity, e.g., *G. verrucosa*. Yamamoto (1975) considered the superficial spermatangial formation of the *Chorda*-Type to be the most primitive, and the other two types (i.e., *Textorii* and *Verrucosa*) in which spermatangial branch systems and conceptacles are formed, more advanced. He found a correlation between the presence of absorbing filaments in the cystocarp and the three types of male organs. The *Chorda* male type always had cystocarps devoid of absorbing filaments, while the *Textorii* male type appeared exclusively in species having cystocarps with absorbing filaments. With the *Verrucosa* male the absorbing filaments were either present or lacking.

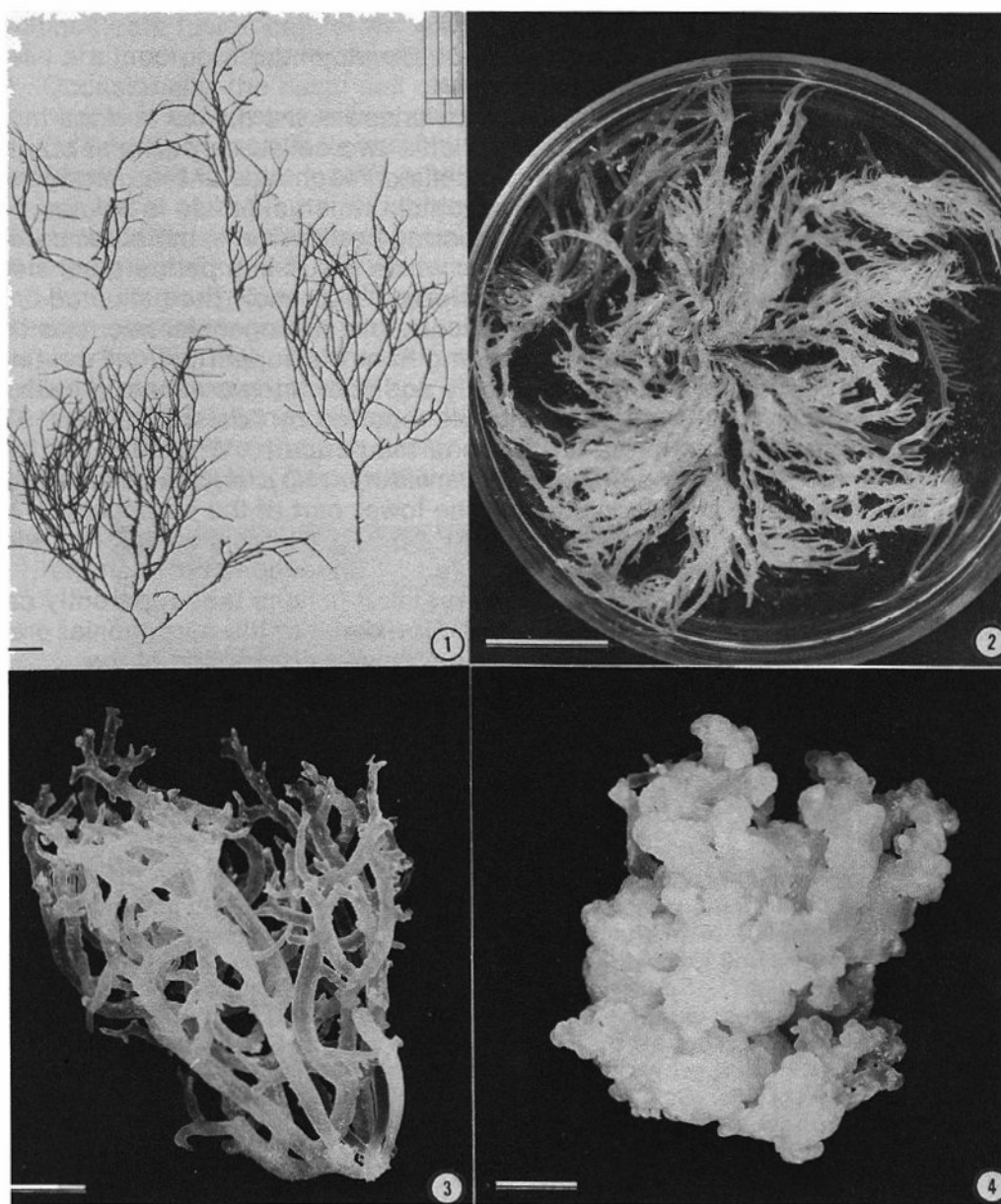
Tetrasporangia develop from primary cortical cells (Sjöstedt 1926; Kylin 1930) and are scattered throughout the cortical layers of the thallus. The meiotic cell divisions in the tetrasporangium result in a cruciate pattern with the tetrasporangium surrounded by narrowly elongated and inwardly curved vegetative cells (Yamamoto 1978).

#### Materials and Methods

Four species were studied: *Gracilaria tikvahiae* McLachlan, 1979, p. 19 (Fig. 1), *Gracilaria cervicornis* (Turner) J. Agardh, 1852, p. 604 (Fig. 2), *Gracilaria debilis* (Forsskal) Børgesen, 1932, p. 7 (Fig. 3), and *Gracilaria crassissima* P. et H. Crouan in Mazé and Schramm 1878, p. 218 (Fig. 4). The taxonomy of Taylor (1960) and McLachlan (1979) was followed.

Specimens were collected by skin- and scuba-diving, and liquid preserved in 5% Formalin—seawater buffered in borax. Some portions of each specimen were dried and pressed on herbarium sheets and cross-referenced to the liquid preserved material. Transverse sections were made through critical developmental stages of carpogonial, cystocarpic, tetrasporangial, and spermatangial structures of each species. All sections were made by hand with a stainless steel single-edge razor blade under a Wild M-5 stereomicroscope at 10X magnification, stained with 1% aqueous aniline blue (following the method of Papenfuss 1937), and permanently mounted on microscope slides in glycerin or in a mixture of 50% Karo Syrup/distilled water with 1% phenol added. Microscopic preparations were examined with a Zeiss Universal or a Leitz Ortholux Microscope. Photographs were taken on the Zeiss Universal Microscope. Specimens studied are deposited in the Algal Collection of the U.S. National Herbarium, National Museum of Natural History, Smithsonian Institution, Washington, D.C. (US).

Specimens studied. *G. tikvahiae*—Florida: Indian River, just north of Link Port Channel jetty, Link Port, 1 m depth, entangled with other algae, coll. J. N. Norris, JN-11627 (female, tetrasporic), 22 Jan 83 (US 94137). *G. cervicornis*—Belize: Carrie Bow Cay, reef flat off north end of island, on coral rubble and shell fragments in sand, depth 0.1–1 m, coll. S. Fredericq and S. M. Lewis, s.n. (female), 11 Apr 83 (US 94140). *G. debilis*—Belize: South Water Cay, 1.5–2 m depth, on coral rubble, coll. J. N. Norris and K. E. Bucher, JN-7351 (female, tetrasporic), 30 Apr 79 (US 94149); coll. R. H. Sims, D-45, 19 Apr 80 (US 94159); coll. J. N. Norris and M. M. Littler, JN-10032, 16 Nov 80 (US 94150); coll. S. Fredericq, G-18 (male), 18 Apr 83 (US 94145); west of reef crest off N.E. side of Cay, 0.3–1.6 m depth, coll. R. H. Sims, G-5 (tetrasporic), 8 Mar 83 (US 94148). Curlew Bank, on coral rubble, 0.4 m depth, coll. S. Fredericq, G-15, 7 Apr 83 (US 94160). Tobacco Reef, between Tobacco Cay and South Water Cay,



**Figs. 1–4. Habits of *Gracilaria* species studied. Fig. 1. *Gracilaria tikvahiae* McLachlan (cystocarpic; US 094137). Fig. 2. *Gracilaria cervicornis* (Turner) J. Agardh (cystocarpic; US 094140). Fig. 3. *G. debilis* (Forsskal) Børgesen (US 094160). Fig. 4. *Gracilaria crassissima* P. et H. Crouan, note parts of anastomosing thallus (US 094157).**

0.5–1.7 m depth, on coral rubble, coll R. H. Sims, 6 Mar 83 (US 94151) and 13 Mar 83 (US 94152). *G. crassissima*—Belize: Curlew Bank, along SE side adjacent to sandy beach, on coral rubble, 0.5–1.3 m depth, 20 Jan 82, coll. R. H. Sims and S. Fredericq (US 94155, tetrasporic; US 94156). South sandbores near Carrie Bow Cay, 0.3 m depth, 8 Jun 1983, coll. S. M. Lewis (US 94146, female; US 94147, female; US 94157, tetrasporic; US 94158, female). Carrie Bow Cay, lagoon side of reef crest, 2 m depth, 11 Mar 83, coll. R. H. and L. Sims (US 94154).



## Results

### 1. Carpogonial Branch and Carposporophyte Development

#### a. *Gracilaria tikvahiae* and *G. cervicornis*

In *G. cervicornis*, the carpogonial branch arises at the thallus surface from a transformed terminal cortical cell that cuts off a two-celled carpogonial branch and a sterile branch of initially one to two cells on each side of the carpogonial branches. In *G. tikvahiae*, once the carpogonial branch expands in volume, becoming distinguishable among its neighboring cortical cells, the outer cortical cells start anticlinal and periclinal divisions which result in a pericarp consisting of several cell layers (Figs. 5–6). In the carpogonial branch, then situated centrally at the base of the developing pericarp, the carpogonium becomes the largest cell (Fig. 6). Cortical branches arising from the supporting cell continue to grow apically to form a cell row terminally and show indeterminate growth, compared to the "typical" sterile branches as reported by Edelstein et al. (1978). Those cell rows contribute to the formation of the pericarp. When the carpogonium has reached a certain size (av. width = 10  $\mu\text{m}$ ), one of the cortical cells at one side of the carpogonium, and the lower part of the carpogonium bend towards each other and form a small connection (Fig. 6). This connection widens and the sterile cells fuse with the carpogonium. Connections between the cortical cells enlarge, resulting in subsequent local fusions that apparently can take place between any cortical cell in close proximity to the carpogonial branch.

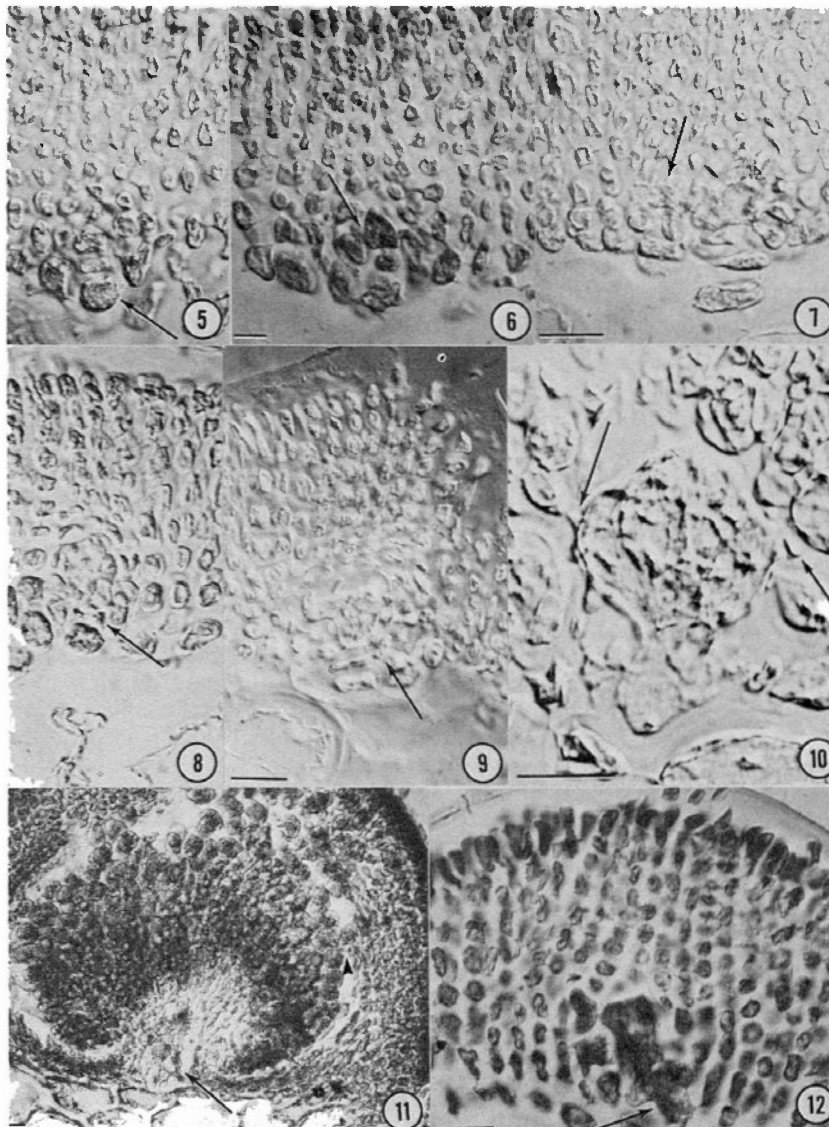
A difference exists between the way the incipient connection of the carpogonium and cortical cells proceeds in *G. tikvahiae* versus *G. cervicornis*. In *G. tikvahiae*, the first fusion movement initiates from a cortical cell in the cell row situated at nearly the same level and height as the carpogonium (Fig. 6). Then the carpogonium further incorporates adjacent cortical cells of the sterile branch laterally and makes extensions towards cells of the pericarp (Fig. 7). A

**Figs. 5–9. Carpogonial branch and carposporophyte development in *G. tikvahiae*.** Fig. 5. Two-celled carpogonial branch consisting of carpogonium and hypogynous cell on supporting cell (arrow). Note short sterile branches are absent, but vegetative cells cut off by the supporting cell grow indeterminately and contribute to pericarp formation (US 094137, slide 4047). Scale bar = 10  $\mu\text{m}$ . Fig. 6. Two-celled carpogonial branch in which the carpogonium expands and makes contact (arrow) with terminal cell of two-celled sterile branch cut off by the supporting cell. Note basal cell of sterile branch cuts off a cell that grows indeterminately, contributing to pericarp formation (US 094137, slide 4046). Scale bar = 10  $\mu\text{m}$ . Fig. 7. Incipient fusion cell formed by expansion of carpogonium and incorporation of cells of sterile branch cut off by supporting cell; hypogynous cell not detectable due to fusion to basal cell of sterile branch; fusion cell makes extensions horizontally (arrow) (US 094137, slide 4052). Scale bar = 20  $\mu\text{m}$ . Fig. 8. Incorporation of cells of the sterile branch which are cut off by the supporting cell into the expanding fusion cell. The hypogynous cell (arrow) has not fused with the basal cells of the sterile branch (US 094137, slide 4049). Scale bar = 15  $\mu\text{m}$ . Fig. 9. Incorporation of basal cell of sterile branch (arrow) fusing with hypogynous cell into expanding fusion cell (US 094137, slide 4050). Scale bar = 20  $\mu\text{m}$ .

**Figs. 10–11. Carposporophyte development in *G. tikvahiae*.** Fig. 10. Young gonimoblast initials cut off at several places from the globose fusion cell (arrows) (US 094137, slide 4048). Scale bar = 25  $\mu\text{m}$ . Fig. 11. Carposporophyte consisting of fusion cell (arrow), gonimoblast cells (placental cells) with carposporangia at the periphery, and absorbing filaments (arrowhead) (US 094137, slide 4052). Scale bar = 20  $\mu\text{m}$ .

**Fig. 12. Carposporophyte development in *G. cervicornis*:** supporting cell and hypogynous cell not distinguishable and seemingly fused. Note extensive fusions at basal cells (arrow). Vegetative cells have fused to each other before becoming part of fusion cell (US 094140, slide 4055). Scale bar = 40  $\mu\text{m}$ .

multinucleate fusion cell forms, which continues to expand until no more cortical cells are incorporated; the hypogynous and supporting cell remain distinct (Fig. 8). Occasionally, the basal cell of the sterile branch fuses with the hypogynous cell, and this fused structure is incorporated into the expanding fusion cell (Fig. 9). Once it has reached its maximum expansion size, the fusion cell begins cutting off gonimoblast initials at different places (Fig. 10). In contrast, it is most likely a basal cell of the sterile branch in *G. cervicornis* that will reach towards and fuse partly with the carpogonium (Fig. 12). Also, several cells are cut off from the supporting cell and form the base of a cell row that expands in diameter and, in fusing with each other, are finally incorporated with the carpogonium. In a more advanced stage, the prominent basal fusions are still recognizable in *G. cervicornis* (Fig. 13). Another difference is found in the fusion cell. It is generally more compact in shape in *G. cervicornis* than in *G. tikvahiae*, because of more fusions among cortical cells which result in the enlargement of the fusion cell. In *G. tikvahiae*, there are relatively fewer fusions between cortical cells, while the input of the carpogonium to the fusion cell is apparently greater.



A cystocarp cavity between pericarp and gonimoblast arises only after the fusion cell has generated gonimoblast initials. The few-celled gonimoblast initials are cut off obliquely from the fusion cell, growing and expanding outwardly. Several subsequent cell divisions form a dense cluster of vacuolate gonimoblast cells (Fig. 10). The expansion of gonimoblast cells proceeds in an irregular fashion. Rows of carposporangia of different sizes, also cut off irregularly, are formed at periphery of these vacuolate cells (Fig. 11). Absorbing filaments originate from the same vacuolate gonimoblast cells that can also cut off carposporangia. There are no absorbing filaments at the base of the cystocarp cavity connecting cortical and placental cells in either *G. cervicornis* or *G. tikvahiae*. The number of pericarp layers increases with the development and expansion of the carposporophyte. The development of the cystocarp in both species is vertical. Because the number of pericarp layers is variable, and not established at the time of carposporophyte initiation, they continue to increase with time, and hence cystocarps of different heights protrude above the thallus surface. An ostiole is not always present in seemingly mature cystocarps.

b. *Gracilaria debilis* and *G. crassissima*

Numerous carpogonial branches were observed immersed at the base of the pericarp in both *G. debilis* and *G. crassissima* (Fig. 14). No cystocarp cavity has developed at this stage, but a distinct boundary line is distinguishable between two zones. The part above the zone of the carpogonial branches is to become the cavity, and distally the pericarp in a strict sense is defined before the development of the gonimoblast. The part below the zone of carpogonial branches is the area below the future cystocarp cavity and is termed the "inner pericarp" following Kraft (1977).

A cortical cell is transformed into a supporting cell which cuts off a carpogonial branch consisting of two cells, the hypogynous cell and the carpogonium. The supporting cell also cuts off sterile branches that flank the carpogonial branch and consist initially of one to two cells (Fig. 15). The inner pericarp, of several layers of small cortical cells (Fig. 16), will play an important role in the development of the gonimoblast. The outer pericarp is present and

**Fig. 13.** Carposporophyte development in *G. cervicornis*: solid fusion cell has incorporated all but the terminal cells of the sterile branch (arrow). Note extensive fusion of vegetative cells at base of fusion cell (US 094139, slide 4054). Scale bar = 30  $\mu\text{m}$ .

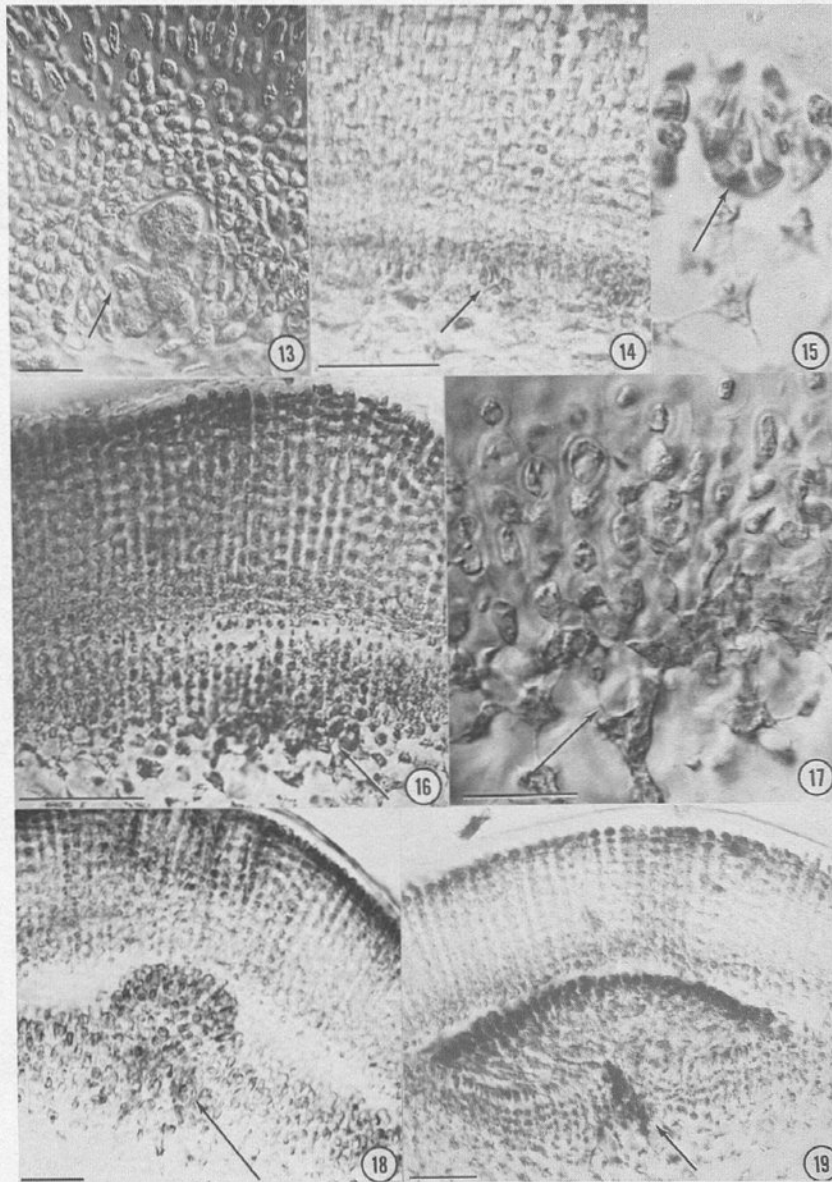
**Figs. 14–17.** Carpogonial branches and carposporophyte development in *G. debilis* and *G. crassissima*. **Fig. 14.** Carpogonial branches (arrow) in *G. debilis* shown at boundary of pericarp and inner pericarp (US 094144, slide 4060). Scale bar = 30  $\mu\text{m}$ . **Fig. 15.** Carpogonial branch apparatus in outer cortex, consisting of a two-celled carpogonial branch cut off by the supporting cell (arrow) and flanked by sterile branches (US 094143, slide 4059). Scale bar = 20  $\mu\text{m}$ . **Fig. 16.** Progressive splitting of pericarp from inner pericarp resulting in the appearance of a cystocarp cavity prior to the presence of gonimoblast initials. Fusion cell (arrow) is embedded in and connected to inner pericarp cells (US 094141, slide 4057). Scale bar = 100  $\mu\text{m}$ . **Fig. 17.** Close up of a fusion cell (an irregular shaped syncytium) connecting (arrow) and fusing to inner pericarp cells (US 094142, slide 4058). Scale bar = 30  $\mu\text{m}$ .

**Fig. 18.** Carposporophyte development in *G. crassissima*. Young gonimoblast originating from inner pericarp cells connected to the fusion cell underneath the cystocarp cavity (arrow). Note the separation of the pericarp from the inner pericarp (US 094138, slide 4053). Scale bar = 70  $\mu\text{m}$ .

**Fig. 19.** Carposporophyte development in *G. debilis*: fusion cell (arrow) connected to inner pericarp cells from which the sporogenous pseudoparenchyma is being cut off forming carposporangia at its periphery. Note that the development of the cystocarp is horizontal (US 094149, slide 4066). Scale bar = 30  $\mu\text{m}$ .



begins to develop prior to the development of the gonimoblast initials or before a fusion cell is distinguishable (Fig. 16). However, a pericarp is not always present when carpogonial branches can be seen (Fig. 15). Although a sterile cell was observed next to the carpogonium, the origin of the fusion cell could not be detected. The fusion cell is an irregularly ramified multinucleate syncytium which expands laterally and connects in several directions to a multitude of adjacent inner pericarp cells (Figs. 16–17). Previous to the splitting of the pericarp, the inner pericarp cells are linked to cells of the pericarp proper. With the appearance of a cystocarp cavity (Fig. 16), the inner pericarp cells become free apically and start to lengthen and expand. Each inner pericarp cell is secondarily pit-connected to other neighboring inner pericarp cells. Each of these cells has the potential to cut off a pseudoparenchymatous tissue thallus-outward. In turn, the pseudoparenchymatous cells cut off more cells, and the whole cell mass results in a sporogenous pseudoparenchyma. We make a



distinction between the term "sporogenous pseudoparenchyma" and "placenta." We call placenta the gonimoblast arising directly from the fusion cell and capable of fusing secondarily with vegetative cells; and sporogenous pseudoparenchyma, the gonimoblast originating indirectly from the fusion cell but from inner pericarp cells which in turn are connected to a fusion cell.

The greater the separation between the pericarp and inner pericarp, the more inner pericarp cells are freed apically to further cut off pseudoparenchyma cells, and the greater the space for gonimoblast expansion (Fig. 18). The gonimoblast originates very early and indirectly from the fusion cell, which is connected to cells of the inner pericarp (Fig. 18). The pseudoparenchyma is of uniform cell size and shape and arises progressively from the inner pericarp cells. On the periphery of this cell mass, short regular rows of carposporangia develop (Fig. 21) without any indication of absorbing filaments connecting to the pericarp (Fig. 19). Proximal to the rows of carposporangia, the pseudoparenchyma is secondarily pit-connected. Short densely staining filaments were frequently present at the base of inner pericarp (Fig. 20) connected to the sporogenous pseudoparenchyma. After the splitting of the pericarp, the pericarp cell layers do not lengthen or increase in height. The number of layers seems to be fixed in early development, at about 13 cell layers. Anticlinal pericarp growth stops and pericarp layers remain constant from the time of carposporophyte initiation until full maturity, so that cystocarp heights in *G. crassissima* and *G. debilis* remain uniform. Since the development of the carposporophyte is principally expansion in width (Figs. 18–19), cystocarps protrude very little above the thallus surface. The gonimoblast develops on a broad base (Fig. 19). An ostiole in the pericarp is only occasionally present, and can be seen in either young or mature cystocarps.

## 2. Tetrasporangia

### a. *Gracilaria cervicornis* and *G. tikvahiae*

In both species the tetrasporangial mother cell is always cut off terminally from a cortical cell and has basal pit-connections. Incurved branchlets encircling the tetrasporangia are common (Fig. 22).

### b. *Gracilaria debilis* and *G. crassissima*

In these two species, the tetrasporangial mother cell is cut off by a cortical cell. The bearing cell can either be a cell of the cortical cell row or a cell at the dichotomy of a cell row. Usually if a tetrasporangial mother cell is borne laterally, having been cut off by a subapical cell, it will have lateral pit-connections (Fig. 23). When the tetrasporangial mother cell is borne terminally, it will have basal pit-connections. The tetrasporangial mother cell, at first quite elongate and thin, expands in diameter as it matures. The cleavage in the tetrasporangium develops in a cruciate manner. Mature tetrasporangia are bright red and ovate in shape.

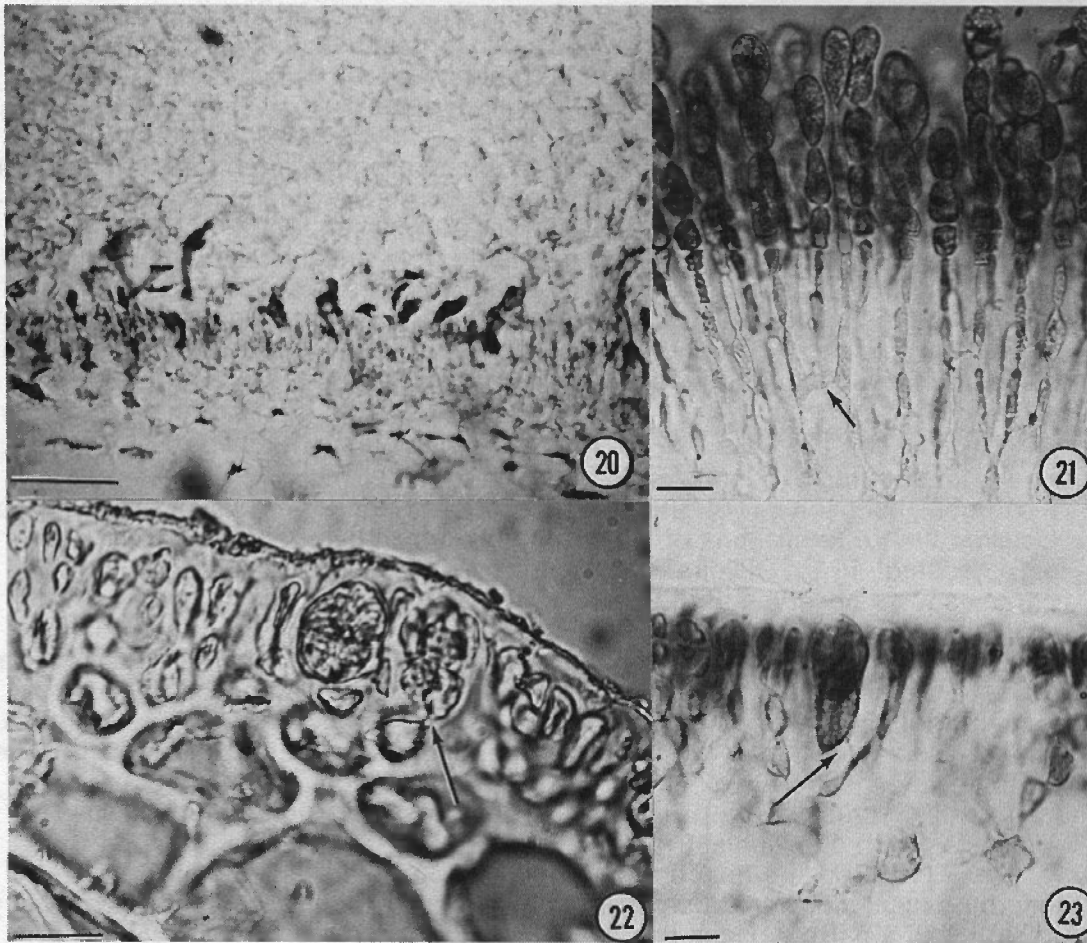
## 3. Spermatangia

### a. *Gracilaria cervicornis*

Spermatangial conceptacles are of the "Textorii-Type" and are formed by the partial conversion of outer cortical cells into spermatangial mother cells. A cortical cell divides, with the resulting outer cell functioning as the spermatangial mother cell. Many such cells, arranged in a horizontal plane, form a shallow depression (Fig. 24). Cortical cells that do not divide into spermatangial mother cells retain their original shape and form the barrier between each conceptacle (Fig. 24). Each spermatangial mother cell cuts off a cell terminally, the spermatangium (Fig. 24). The spermatangial conceptacles are relatively shallow; a surface view shows both spermatangial and cortical cells in the same focal depth.

### b. *Gracilaria debilis* and *G. crassissima*

In these species, the cortical cell rows divide, with some transforming into



**Figs. 20–21.** Carposporophyte development in *G. crassissima*. **Fig. 20.** Short connecting filaments connect inner pericarp cells to sporogenous pseudoparenchyma (US 094146, slide 4063). Scale bar = 20  $\mu\text{m}$ . **Fig. 21.** Sporogenous pseudoparenchyma is secondarily pit-connected (arrow), but not the rows of carposporangia (US 094147, slide 4064). Scale bar = 25  $\mu\text{m}$ .

**Figs. 22–23.** Tetraspore development in *G. cervicornis* and *G. crassissima*. **Fig. 22.** Tetrasporic cortex in *G. cervicornis*. Tetrasporangium after the transverse division is cut off terminally from the tetrasporangial mother cell (arrow) (US 094138, slide 4053). Scale bar = 30  $\mu\text{m}$ . **Fig. 23.** Young tetrasporangium originating laterally in *G. crassissima* from cortical bearing cell (arrow) (US 094148, slide 4065). Scale bar = 10  $\mu\text{m}$ .

small rows of spermatangial mother cells all of which initially are connected to each other (Fig. 26). It appears that any cortical, subcortical, or medullary cell may be capable of dividing and being transformed into a spermatangial mother cell. However, the growth and shape of the conceptacles when they originate deep inside the thallus is restricted to the outline and shape of the medullary cells. The medullary cells are connected to each other in a cuboidal or pentagonal pattern, which forms the configuration of the conceptacles (Fig. 25). The configuration of male conceptacles embedded in the cortex, subcortex, or medulla is extremely variable. When several pentagonal-shaped medullary cells cut off simultaneously in close proximity small cells that function as

spermatangial mother cells, then adjacent, compound internal spermatangial conceptacles are formed (Fig. 26). If all the cortical cells outward of the developing conceptacle divide and are transformed into the spermatangial mother cells, an outer cortical cell layer will be absent (Fig. 25, right). However, when these cortical cell layers are not dividing, they enclose the outside of the spermatangial conceptacle (Fig. 25, left). Eventually, the outer cortical cell layers divide, thus opening a space that functions as a pore through which the mature spermatangia may be released. In a surface view, when a pore is present, the spermatangial conceptacles are differentiated from the surrounding cortical cells by the presence of deep holes. In contrast, if the pore is absent, only cortical cells will be distinguishable, concealing the maturing conceptacle underneath. Because of this cryptic manner of conceptacle development in the young phases, male plants are difficult to identify in these species.

### Discussion

An interesting taxonomic problem about the development of the pericarp reemerges. Johnson's (1888) interpretation that pericarp formation in *Gracilaria* occurred *before* fertilization of the carpogonium has been considered incorrect (e.g., Sjöestedt 1926; Oliveira 1969). However, in this study, carpogonial branches were observed at the boundary of pericarp and inner pericarp in *G. debilis* and *G. crassissima* without any detection of having been fertilized, thus supporting Johnson's conclusion based on his work on *G. confervoides*. In order to insure transfer of nutrients from the fusion cell to the carposporangia, it appears that either a large centralized fusion cell is necessary, or a very diffuse, ramified fusion cell that is pit-connected to a multitude of neighboring cells. The first pathway is shown in *G. cervicornis* and *G. tikvahiae*, and the second in *G. debilis* and *G. crassissima*. The result in both cases, though from different origins, is a rich gonimoblast.

Ohmi (1958) made the correlation that with a broad-based gonimoblast, absorbing filaments were absent, and that these absorbing filaments were mostly present with a narrow-based gonimoblast. [However, *G. lemaneiformis* has a narrow base and *no* absorbing filaments (I. A. Abbott, personal communication).] Ohmi's observations are corroborated in this study; *Gracilaria debilis* and *G. crassissima* have a broad-based gonimoblast devoid of absorbing filaments. In contrast, *G. tikvahiae* and *G. cervicornis* have a narrow-based gonimoblast with absorbing filaments. Ohmi did not, however, document the development of the fusion cell.

The nature of the fusion cell is the prime reproductive feature around which the other features, such as presence or absence of absorbing filaments, are formed. It has been generally assumed that the absorbing filaments have a nutritive function of connecting the assimilatory layers and conveying the photosynthetic products to the developing gonimoblast. (This assumes that they originate in the pericarp.) In *G. crassissima* and *G. debilis* such absorbing filaments are absent. If a nutritive role is assumed for the absorbing filaments, then no specialized supplementary means to transfer nutrients to the developing gonimoblast would be necessary: the small filaments connecting inner pericarp cells to the sporogenous pseudoparenchymatous tissue in *G. debilis* and *G. crassissima* probably are sufficient for nutrient transfer to the developing carposporangia. Because of the early progressive splitting of the pericarp, the cystocarp cavity is not spatially restricted in width for liberation of carpospores. In contrast, in *G. cervicornis* and *G. tikvahiae*, absorbing filaments are present and always originate late in the development of the cystocarps. Another possible role of the absorbing filaments could be biochemical. The absorbing filaments (if they originate in the gonimoblast) may produce a chemical, perhaps an enzyme,



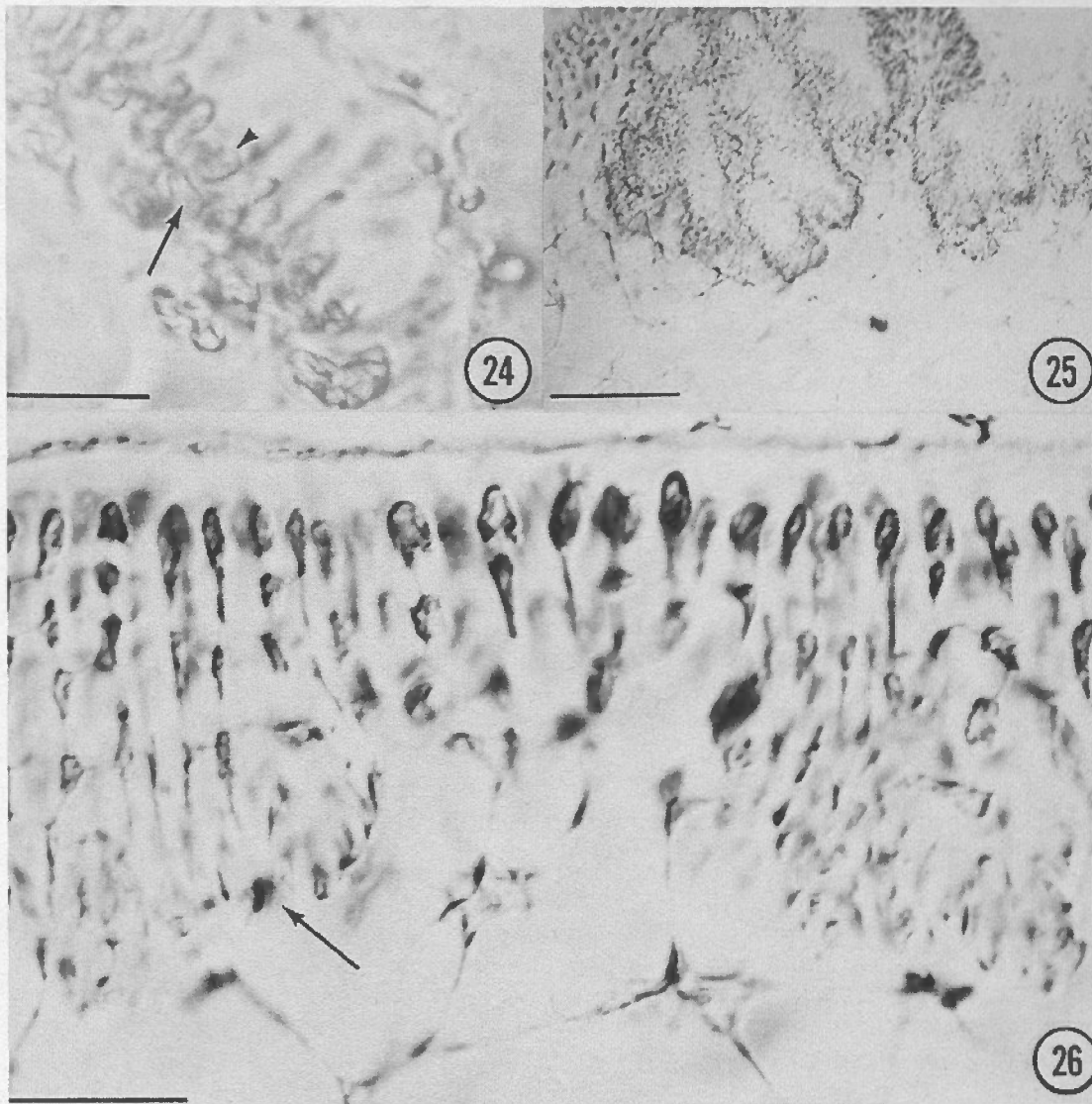


Fig. 24. Spermatangia of *G. cervicornis*, immersed in shallow conceptacles flanked by cortical cells. Spermatangial mother cells (arrow) and spermatangia (arrowhead) are distinguished (US 094139, slide 4054). Scale bar = 30  $\mu\text{m}$ .

Fig. 25. Deeply immersed spermatangial conceptacles of *G. debilis*: cortical cells above conceptacles have completed division (right) while those on the left have not yet divided. Thus, a pore (right) is present or absent (left) (US 094145, slide 4062). Scale bar = 60  $\mu\text{m}$ .

Fig. 26. Spermatangial mother cells of *G. crassissima* and *G. debilis* (arrow) do not originate from one outer cortical cell, but from a string of deep cortical-medullary cells (e.g., *G. debilis*, US 094145, slide 4061). Scale bar = 30  $\mu\text{m}$ .

which, upon penetrating the pericarp, could stimulate the expansion of the pericarp, thus widening a space between the sporangial mass and the pericarp. This would provide enough space for carposporangial enlargement and release through the ostiole. It is possible that, as the cystocarp develops in height, space is needed for the carposporangia to grow upward since there is no space available for the gonimoblast to expand further laterally. Absorbing filaments are



prevalent in cystocarps when the height of the cystocarp exceeds the width (e.g., *G. cervicornis* and *G. tikvahiae*), and tend to be absent when the width exceeds the height (e.g., *G. debilis* and *G. crassissima*).

Since the absorbing filaments originate from gonimoblast tissue, it can be assumed that a specific cystocarp will not have both types of filaments. Only one type is present, such as the "classic" absorbing filaments connecting gonimoblast to pericarp, or the other type, in which short filaments connect the inner pericarp cells to sporogenous pseudoparenchymatous tissue (see also Chang and Xia, 1963, fig. 7). In the specimens studied, presence or absence of absorbing filaments can be predicted based on the nature of gonimoblast origin: if the gonimoblast originates directly from the fusion cell, and immediately starts developing outward from the thallus prior to the occurrence of a cystocarp cavity, absorbing filaments will be present. On the other hand, if the gonimoblast originates indirectly from the fusion cell as sporogenous pseudoparenchyma from the inner pericarp cells, and the cystocarp cavity originates very early, then short filaments between the inner pericarp cells penetrating the pseudoparenchyma can be expected. A third option is that neither absorbing filaments nor "basal absorbing filaments" (the latter type are on the inner pericarp cells) are present [see e.g., *Gracilariopsis sjoestedii* (Kyllin) Dawson, 1949, pl. 17, fig. 5].

A cortical cell in the region of developing tetrasporangia has the potential to cut off cells terminally as well as cutting off another cell laterally. For example in *G. debilis* and *G. crassissima*, if a tetrasporangial mother cell originates laterally from its bearing cell, cortical cells can originate terminally from the same bearing cell. This is apparently the first report in *Gracilaria* of lateral development of tetrasporangia from bearing cells. In another family of the Gigartinales, the Solieriaceae, a lateral or terminal origin of tetrasporangia was a prime character used for segregating major tribes (Gabrielson and Hommersand, 1982a,b).

Similarly, if a carpogonial branch is cut off terminally from a cortical cell, then that cortical cell will only cut off carpogonial branch initials and adjacent sterile cells. If, however, the carpogonial branch initial is cut off more laterally from a bearing cell, then that bearing cell can still cut off a cell row terminally. The result is that the carpogonial branches may not appear terminally immersed in the outer cortex, but rather in the subcortex. The carpogonial branches can then be present at the base of the pericarp or just underneath the cystocarp cavity, as was observed in *G. debilis* and *G. crassissima*.

When cells are cut off laterally in the development of spermatangia in *Gracilaria*, compound spermatangial conceptacles can be expected. Børgesen (1953) commented on the fact that an ostiole was absent in the compound, deeply imbedded conceptacles of *G. multifurcata* Børg. [= *Polycavernosa multifurcata* (Børg.) Chang et Xia, 1963]. Ohmi (1958b) found the same aberrant spermatangial (as "antheridial") conceptacles in *G. henriquesiana* Hariot from the Gold Coast, Africa. This type of spermatangial conceptacle was the primary basis for segregation of a new genus, *Polycavernosa* Chang et Xia (1963, p. 120), based on *P. fastigiata* Chang et Xia. This unusual development of spermatangia, which does not arise from one terminal cortical cell, was observed in our specimens of *G. debilis* and *crassissima*, and is fundamentally different from the "Textorii-Type" shown by *G. cervicornis*.

The inherent plasticity in the nature of cell divisions (anticlinal vs. periclinal) and the implications for cutting off various types of reproductive cells (e.g., carpogonial branch, tetrasporangium, or spermatangia) are derived from a differential capacity of cells to form secondary pit-connections with neighboring cells. All *Gracilaria* species in this study formed secondary pit-connections. However, the degree to which species have potential and plasticity to form secondary pit-connections must be tested as a basis for taxonomic evaluation of

species groupings. It is obvious that the ability of *G. debilis* and *G. crassissima* to form secondary pit-connections is greater than that of *G. tikvahiae* or *G. cervicornis*. There is probably greater fertilization efficiency from an array of vegetative cells that have the ability to connect very closely either to other cortical cells or to a carpogonium (resulting in a large fusion cell), without the need for auxiliary cell filaments as seen in other families of Gigartinales (e.g., Solieriaceae J. Agardh). The phylogenetic affinities of the Gracilariaceae at the familial and ordinal levels remain to be clarified.

### Summary

Developmental sequences of post-fertilization events reveal two developmental patterns within the genus *Gracilaria*, which are proposed to represent two distinct groups: *Group 1*—*G. debilis* and *G. crassissima*, and *Group 2*—*G. cervicornis* and *G. tikvahiae*.

**Table 1. Comparison of Reproductive Features of *Gracilaria* Group 1 (=Polycavernosa) vs. Group 2 (=Gracilaria).**

	GROUP 1: <i>G. debilis</i> (Forssk.) Bórg. and <i>G. crassissima</i> P. et H. Crouan	GROUP 2: <i>G. cervicornis</i> (Turn.) J. Ag. and <i>G. tikvahiae</i> McLachlan
Timing and Origin of the Gonimoblast	develops early, from inner pericarp cells connected to the fusion cell; i.e., <i>indirect</i> from the fusion cell; space forms between pericarp and future gonimoblast <i>before</i> fusion cell incorporates adjacent cortical cells.	develops late, <i>direct</i> from the fusion cell; no space between pericarp and future gonimoblast until <i>after</i> fusion cell incorporates adjacent cortical cells.
Direction of Cystocarp Development	mainly horizontal; thus cystocarp growth is in width.	mainly vertical; thus cystocarp growth is in height.
Mature Cystocarp Shape	low, wide, and $\pm$ flat.	tall and $\pm$ pyramidal.
Nature of Pericarp	present before expansion of fusion cell; number of pericarp cell layers apparently fixed in early development; cystocarps $\pm$ uniform in height.	formed concomitant with development and expansion of fusion cell; number of pericarp cell layers not fixed; cystocarps of various heights.
Cystocarp Cavity	present <i>before</i> development of gonimoblast initials.	present, only <i>after</i> appearance of gonimoblast initials.
Fusion Cell Shape	ramified, spreading; not easily distinguished.	unbranched, appears "solid"; prominent.
Absorbing Filaments	absent	present
Origin of Spermatangia	from cortical or subcortical/medullary cells.	only from cortical cells.
Origin of Tetrasporangia	terminal or lateral from a cortical cell.	only terminal from a cortical cell.

This generic complex of taxa is unique in having both a fusion cell and placental or pseudoparenchymatous cells in their respective cystocarps. Based on the material studied, there has been a significant divergence in the gonimoblast origin and in the developmental sequence shown by these two groups. Presence or absence of the other secondarily developed cystocarp features seem to develop around this basic difference in gonimoblast origin. Once the gonimoblast origin is established, the subsequent development can be predicted in the tropical and subtropical western Atlantic species we studied.

In the "classic" *Gracilaria* concept of Sjöstedt (1926) the gonimoblast originates directly from the fusion cell. This direct origin was found in *Group 2*, *G. cervicornis* and *G. tikvahiae*. In *Group 1*, *G. debilis* and *G. crassissima*, the gonimoblast does not originate directly, but rather indirectly from the fusion cell. The uniqueness of *Group 1* lies in the fact that a space forms between the pericarp and the future gonimoblast before the fusion cell incorporates adjacent cortical cells. Fundamental differences useful for taxonomic separation of the two groups are summarized in Table 1. The taxonomic significance of these differences in reproductive morphology was considered. At this point we suggest that the two distinct developmental pathways of these two groups represent two separate genera. A thorough investigation of reproductive structures and their developmental origins and sequences must be studied in the generic types of *Gracilaria*, *Gracilariopsis*, and *Polycavernosa* to reveal where *Group 2* belongs. We recognize that the species of *Group 2* are more closely aligned with the "classic" concept of *Gracilaria* (*sensu* Sjöstedt 1926). Studies are now in progress comparing developmental patterns of the reproductive structures of *Polycavernosa fastigiata* (from type locality) with our *Group 1*. At this time, based on our observations on the type and origin of the spermatangial conceptacles and the features of the mature cystocarps in our Caribbean specimens of *G. debilis* and *G. crassissima* being the same as described for *Polycavernosa* by Chang and Xia (1963), we propose the following new combinations:

*Polycavernosa debilis* (Forsskål) Fredericq et J. Norris, comb. nov. Basionym: *Fucus debilis* (Forsskål) 1775, p. 191. Synonym: *Gracilaria debilis* (Forsskål) Brørgesen 1932, p. 7.

*Polycavernosa crassissima* (P. et H. Crouan) Fredericq et J. Norris, comb. nov. Basionym: *Gracilaria crassissima* P. et H. Crouan in Mazé and Schramm 1878, p. 218 (date of publication *vide* Stafleu and Cowan 1981, p. 392).

The recognition of these two groups is a contribution that we believe will help to clarify generic concepts and species limits in a taxonomically difficult but economically important group of red algae. We encourage that detailed studies be undertaken of type locality material of *Gracilaria* taxa to avoid nomenclatural problems and misidentifications.

#### Acknowledgements

This paper in part represents a portion of a thesis that was submitted by S. Fredericq in partial fulfillment of the M.S. degree to George Mason University (Fairfax, Virginia). Participation of S. Fredericq in the "Sea Grant Economic Algae Workshop" (held at the University of Guam) was made possible by a National Museum of Natural History (NMNH) Travel Grant to JN; we thank Richard Fiske (Director, NMNH) for his support. For critical reviews of this paper we thank I. A. Abbott, H. Yamamoto, K. E. Bucher, C. E. Jones, and D. P. Kelso; and for informative discussion during the Guam Workshop we are grateful to I. A. Abbott, Y. M. Chiang, M. S. Doty, R. T. Tsuda, T. Yoshida, and especially Xia Bangmei. For assistance in collecting material studied in Belize we thank R. H. Sims, S. M. Lewis, K. E. Bucher, and M. M. Littler; and in Florida, M. D. Hanisak and S. M. Blair. This study is contribution number 152 of the "Smithsonian Institution's Coral Reef and Mangrove Program," supported in part by a grant from the Exxon Corporation Foundation; we are

grateful to K. Rützler (Program Manager) for logistical support. Funding for the Florida research was through a grant to J. Norris from the Smithsonian Marine Station at Link Port, and represents contribution number 141.

#### Literature Cited

- Abbott, I. A. 1972. Field studies which evaluate criteria used in separating species of *Iridaea* (Rhodophyta). In: Abbott, I. A. and Kurogi, M. (eds.), Contributions to the Systematics of Benthic Marine Algae of the North Pacific, pp. 253–264. Kobe, Japan: Japan. Soc. Phycol.
- . 1983. Some species of *Gracilaria* (Rhodophyta) from California. *Taxon* 32(4): 561–564.
- Agardh, J. G. 1852. Species, genera et ordines Algarum. C. W. K. Gleerup, Lund. II(ii): 337–720.
- Bird, C. J. and McLachlan, J. 1982. Taxonomy of *Gracilaria*: Taxonomic criteria in *Gracilaria* (Rhodophyta, Gigartinales). *Bot. Mar.* 25: 557–562.
- . 1984. Taxonomy of *Gracilaria*: Evaluation of some aspects of reproductive structure. *Hydrobiologia* 115/116:41–62.
- Bodard, M. 1964. Le *Gracilaria occidentalis* (Bör.) : Une espèce de Rhodophycée pantropicale Atlantique. *Bull. Mus. Nat. d'Hist. Nat.* 2(36)6: 874–878.
- . 1967. Sur le développement des cystocarpes des *Gracilaria* et *Gracilariopsis* au Sénégal. *Bull. de l'I. F. A. N.* 29(A)3: 879–897.
- Börjesen, F. 1932. A revision of Forsskal's algae, mentioned in Flora Aegyptiaco-Arabica and found in his herbarium in the Botanical Museum of the University of Copenhagen. *Dansk Bot. Arkiv* 8(2): 1–14, 1 pl.
- . 1950. Some marine algae from Mauritius. Additions to the parts previously published, II. *Det Kgl. Danske Vidensk. Selskab, Biol. Medd.* 18(11): 1–46.
- . 1953. Some marine algae from Mauritius. Additions to the parts previously published, V. *Det Kgl. Danske Vidensk. Selskab, Biol. Medd.* 21(9): 1–62.
- Chang C. F. and Xia Bangmei. 1963. *Polycavernosa*, a new genus of the Gracilariaceae. *Stud. Mar. Sinica* 3:119–126, pls. 1–2.
- . 1964. A comparative study of *Gracilaria foliifera* (Forssk.) Bör. and *Gracilaria textorii* (Suring.) DeTonl. *Acta Bot. Sinica* 12(2): 201–209.
- . 1976. Studies on Chinese species of *Gracilaria*. *Stud. Mar. Sinica* 11: 91–163, pls. 1–2.
- Chapman, A. R. O., Edelstein, T. and Power, P. J. 1977. Studies on *Gracilaria*. I. Morphological and anatomical variation in samples from the Lower Gulf of St. Lawrence and New England. *Bot. Mar.* 20: 149–153.
- Dawson, E. Y. 1949. Studies on the Northeast Pacific Gracilariaceae. Allan Hancock Found. Publs., Occ. Papers 7:1–54.
- Delivopoulos, S. G. and Tsekos, I. 1983. A light microscope study of carposporophyte development in *Gracilaria verrucosa* (Hudson) Papenfuss. *Ann. Bot.* 52(3): 317–323.
- Diaz-Piferrer, M. and Caballer de Perez, C. 1964. Taxonomia, ecología y valor nutricional de alga marinas de Puerto Rico: Algas productoras de agar. *Admin. Fomento Economico, Hato Rey, P. R.* 145 pp.
- Edelstein, T., Chen, L. C. M. and McLachlan, J. 1978. Studies on *Gracilaria* (Gigartinales, Rhodophyta): Reproductive structures. *J. Phycol.* 14: 92–100.
- Forsskal, P. 1775. Flora Aegyptiaco-Arabica. Sive descriptiones plantarum, quas Aegyptum inferiorem et Arabiam felicem detexit, illustravit Petrus Forsskal. Möller, Kjøbenhavn. 32, 219 pp., map.
- Gabrielson, P. W. and Hommersand, M. H. 1982a. The Atlantic species of *Solieria* (Gigartinales, Rhodophyta). II. Their morphology, distribution and affinities. *J. Phycol.* 18: 31–45.
- . 1982b. The morphology of *Agardhiella subulata* representing the Agardhielleae, a new tribe in the Solieriaceae (Gigartinales, Rhodophyta). *J. Phycol.* 18: 45–58.
- Grieg-Smith, E. 1954. Cytological observations on *Gracilaria multipartita*. *Brit. Phycol. J.* 2:4–5.
- Greville, R. K. 1830. *Algae Britannicae*. Edinburgh, Scotland, 218 pp., 19 pls.
- Hay, M. E. and Norris, J. N. 1984. Seasonal reproduction and abundance of six sympatric species of *Gracilaria* Grev. (Gracilariaceae; Rhodophyta) on a Caribbean subtidal sandplain. *Hydrobiologia* 116/117: 63–94.

- Hoyle, M. D. 1978. Reproductive phenology and growth rates in two species of *Gracilaria* from Hawaii. *J. Exp. Mar. Biol. Ecol.* 35: 273–283.
- . 1984. Taxonomic features used in discriminating some central and eastern Pacific species of *Gracilaria*. *Hydrobiologia* 116/117: 47–50.
- Johnson, T. 1888. The procarpium and fruit in *Gracilaria confervoides*, Grev. *Ann. Bot.* 3–4: 213–222.
- Kraft, G. T. 1977. Transfer of the New Zealand red alga *Tylopus proliferus* (Gracilariaceae, Gigartinales) to the genus *Gracilaria*. *New Zealand J. Bot.* 15: 495–502.
- Kylin, H. 1930. Über die Entwicklungsgeschichte der Florideen. *Lunds Univ. Årsskr. N.F. Avd. 2*, 26(6): 1–104.
- Mazé, H. and Schramm, H. 1878 [1870–1877]. *Essai de classification des algues de la Guadeloupe*. (2nd edition). xix, 283, [iii] pp. Basse-Terre, Guadeloupe: Imprimerie du Gouvernement.
- McLachlan, J. 1979. *Gracilaria tikvahiae* sp. nov. (Rhodophyta, Gigartinales, Gracilariaceae) from the Northwestern Atlantic. *Phycologia* 18(1): 19–23.
- Mikami, H. 1965. A systematic study of the Phylloporaceae and Gigartinaceae from Japan and its vicinity. *Scient. Papers Instit. Algal. Research, Fac. of Sci., Hokkaido Univ.* 5(2): 181–285, 11 pls.
- Newton, L. M. 1953. Marine algae. *John Murray Exped. Scient. Rept.* 9(5): 395–420.
- Ohmi, H. 1958a. The species of *Gracilaria* and *Gracilariopsis* from Japan and adjacent waters. *Mem. Fac. Fish., Hokkaido Univ.* 6: 1–66.
- . 1958b. On aberrant antheridial conceptacles found in *Gracilaria henriquesiana* Hariot from the Gold Coast, Africa. *Bull. Jap. Soc. Phycol.* 6(1): 4–7.
- Oliveira, J. C. 1969. Recherches sur le développement et les organes reproducteurs des *Gracilaria* de la Manche. *Rev. de Scienc. Biol.* A(2): 11–49.
- Oliveira, E. C. de, Bird, C. J. and McLachlan, J. 1983. The genus *Gracilaria* Greville (Rhodophyta, Gigartinales): the Western Atlantic *D. domingensis* Sonder ex Kütz., *pro syn.*, *G. cervicornis* (Turner) J. Ag. and *G. ferox* J. Ag. *Can. J. Bot.* 61(12): 2999–3008.
- Ortiz Sotomayor, A. 1976. The genus *Gracilaria* (Gigartinales: Gracilariaceae) in Puerto Rico: Taxonomy and ecology. Unpubl. Ph.D. dissertation, Universidad de Puerto Rico, Mayaguez. 196 pp., 19 illust.
- Ortiz Sotomayor, A. and Almodovar, L. R. 1982. El genero *Gracilaria* (Gigartinales: Rhodophycophyta) en Puerto Rico y su posible potencial como agarophyto a escala industrial. *Caribb. J. Science* 18: 1–4.
- Oza, O. M. 1976. Studies on Indian *Gracilaria*. II. The development of reproductive structures of *Gracilaria corticata*. *Bot. Mar.* 19: 107–114.
- Papenfuss, G. F. 1935. The development of the gonimoblast in *Melanthalia abscissa*. *Kungl. Fysiol. Sällsk., I, Lund Forhandl.* 5(15):1–10.
- . 1937. The structure and reproduction of *Claudea multifida*, *Vanvoorstia spectabilis*, and *Vanvoorstia coccinea*. *Symb. Bot. Ups.* 2(4): 1–66.
- . 1953. Outstanding problems in the morphology and taxonomy of marine algae of the tropical and south Pacific. *7th Pacif. Sci. Congress* 5:27–39.
- . 1967. Notes on Algal Nomenclature—V. Various Chlorophyceae and Rhodophyceae. *Phycos* 5(1–2): 95–105.
- Phillips, R. W. 1925. On the origin of the cystocarp in the genus *Gracilaria*. *Ann. Bot.* 39(156):787–803.
- Schmitz, F. 1889. Systematische Übersicht der bisher behannten Gattungen der Florideen. *Flora* 72:435–456, pl. 21.
- Schneider, C. W. 1975. Taxonomic notes on *Gracilaria mammillaris* (Mont.) Howe and *Gracilaria veleroae* Dawson (Rhodophyta, Gigartinales). *Taxon* 24:643–646.
- Silva, P. C. 1980. Names of classes and families of living algae. *Regnum Vegetabile* 103:1–156.
- Sjöstedt, L. G. 1926. Floridean Studies. *Lunds Univ. Årsskr. N.F. Avd. 2*(22):1–94, figs. 1–41.
- Stafleu, F. A. and Cowan, R. S. 1981. *Taxonomic literature...Vol. III: Lh-O* (2nd ed.) xii, 980 pp. Utrecht: Bohn, Scheltema & Holkema [Regnum Vegetabile 105].
- Taylor, W. R. 1960. Marine algae of the eastern tropical and subtropical coasts of North America. *Univ. Michigan Press, Ann Arbor.* 870 pp.
- . 1969. Notes on the distribution of West Indian marine algae, particularly in the Lesser Antilles. *Contr. Univ. Mich. Herb.* 9(2):125–203.



- Thuret, G. and Bornet, E. 1878. Etudes phycologiques. Paris. iii, 105 pp., 51 pl.
- Trono, Jr., G. C. and Azanza-Corrales, R. 1981. The seasonal variation in the biomass and reproductive states of *Gracilaria* in Manila Bay. In: Levring, T. (ed.), Proc. Xth International Seaweed Symposium pp. 743–748. Walter de Gruyter & Co., Berlin and New York.
- Trono, G. C., Azanza-Corrales R. and Manuel, D. 1983. The genus *Gracilaria* Gigartinales, Rhodophyta) in the Philippines. Kalikasan, Philipp. J. Biol. 12(1–2):15–41.
- Turner, D. 1809. Fuci, sive plantarum fucorum generi a botanicis ascriptarum, icones, descriptiones et historia. 2:72–134. J. & A. Arch, London.
- Umamaheswara Rao, M. 1972. On the Gracilariaceae of the seas around India. J. Mar. Biol. Ass. India. 14(2):671–696.
- . 1973. Growth and reproduction in some species of *Gracilaria* and *Gracilariopsis* in the Palk Bay. Indian J. Fish. 20:182–192.
- Vélez Villamil, S. M. 1981. El cultivo de *Gracilaria domingensis* (Kützinger) Sonder ex Dickie. Unpubl. MS thesis, Univ. Puerto Rico, 105 pp.
- Yamamoto, H. 1975. The relationships between *Gracilariopsis* and *Gracilaria* from Japan. Bull. Fac. Fish., Hokkaido Univ. 26: 217–222.
- . 1978. Systematical and anatomical study of the genus *Gracilaria* in Japan. Mem. Fac. Fish., Hokkaido Univ. 25(2):97–152.
- Yang, H. N. and Chiang, Y. M. 1982. Taxonomical study of the *Gracilaria* of Taiwan. Journ. Fisheries Soc. Taiwan. 9(1–2):55–71.