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STUDIES ON CYLINDRICAL SPECIES OF WESTERN ATLANTIC *GRACILARIA* (GRACILARIALES, RHODOPHYTA): *G. CYLINDRICA* BØRGESEN AND *G. BLODGETTII* HARVEY

Suzanne Fredericq and James N. Norris

Abstract

Studies of two western Atlantic species of *Gracilaria* have shown that *G. cylindrica* Børgesen, described from between St. Jan (St. John) and St. Thomas, Virgin Islands, is conspecific with *G. blodgettii* Harvey, a taxon originally described from Key West, Florida. On the basis of an analysis of topotype material and recent liquid-preserved spermatangial and cystocarpic collections from Puerto Rico, we found no inherent differences to support treating these two entities as distinct taxa. Special attention was focused on analyzing in detail the developmental sequence of spermatangial parent cells. Using recent collections of *G. blodgettii* from Puerto Rico, we photographed and diagrammed on a cell-by-cell basis the origin of spermatangial parent cells leading to the characteristic very shallow *textorii*-type male sori. The oldest validly published name for this species is *G. blodgettii* Harvey (1853) vs *G. cylindrica* Børgesen (1920).

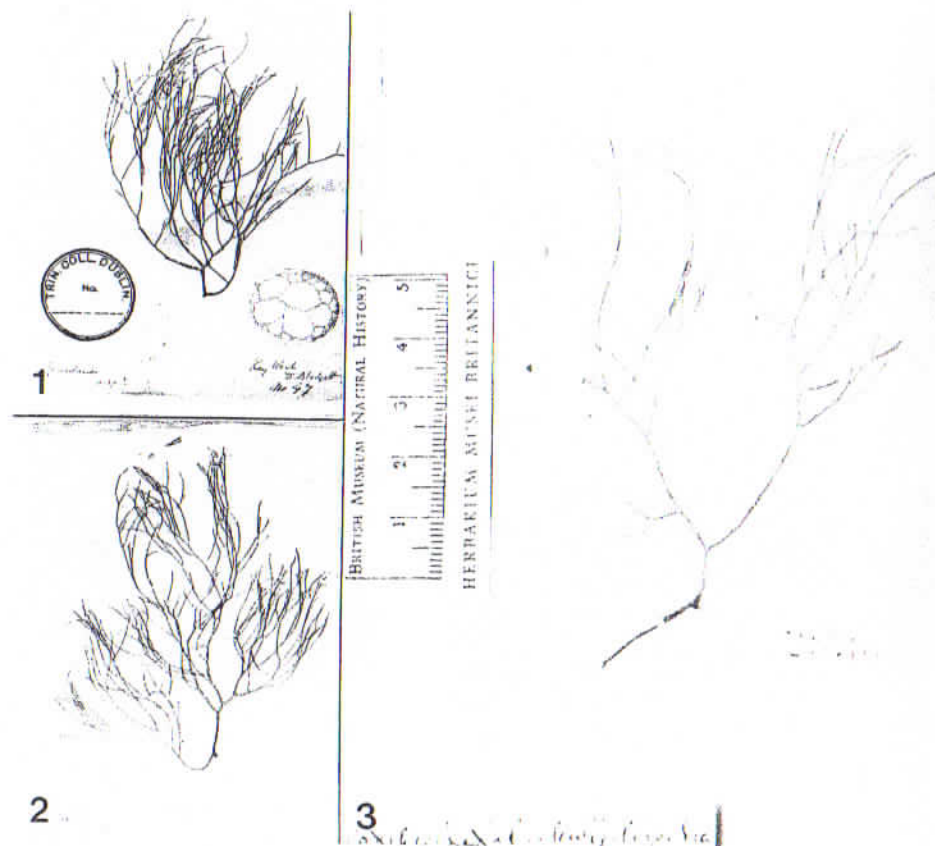
Introduction

In most floristic treatments and checklists, *G. blodgettii* Harvey (Harvey 1853, p. 111) and *G. cylindrica* Børgesen (Børgesen 1920, p. 375) are viewed as separate species (e.g., Taylor 1960, Ortiz Sotomayor 1976, Almodovar and Ballantine 1983, Wynne 1986). To some authors, however, the distinction between these two terete taxa is less evident. For example, Chapman (1963) noted that specimens of *G. blodgettii* from Jamaica graded into *G. cylindrica* and a species he referred to as *G. verrucosa*, and are difficult to assign. Yamamoto (1985) also thought that these Caribbean species appeared closely related. Earlier, Taylor (1960) pointed out that some specimens of *G. cylindrica* were perhaps intermediate with *G. blodgettii*. Because of these conflicting taxonomic interpretations in the literature, we investigated whether *G. blodgettii* and *G. cylindrica* as found in the Caribbean are distinct or possibly the same taxon.

Gracilaria (?) *blodgettii* was described by Harvey (1853), who was not sure of its generic placement; the description was based on specimens collected by Dr. Blodgett from Key West, Florida Keys, Florida. Diagnostic for this new species were branches and branchlets being constricted at their base of insertion and attenuated to an acute point; a medulla consisting of a few very large, thin-walled, irregularly polygonal cells; and a cortex of vertically subseriate, very small, pigmented cells. The lectotype specimen of *G. blodgettii* is housed in Trinity College, Dublin (TCD; Fig. 1); isolectotype specimens are in TCD (Fig. 2; tetrasporangial thallus, C. J. Bird annotation) and in the Agardh Herbarium, Lund (LD 29309) (Fig. 3).

Børgesen (1920) described *G. cylindrica* on the basis of cystocarpic and tetrasporangial deep-water specimens from "many places in the sound between St. Jan [St. John] and St. Thomas; and in the sea to the north of American Hill," Virgin Islands. Børgesen was of the opinion that *G. cylindrica* resembled *G. blodgettii* in having basally constricted branches and a terete habit but differed in being less densely ramified and having obtuse rather than acute branch apices. Lectotypic (Fig. 4) and isolectotypic specimens (e.g., Fig. 5) are located in Copenhagen (C), and a syntypic specimen is housed in Leiden (L-1841) (Fig. 6).

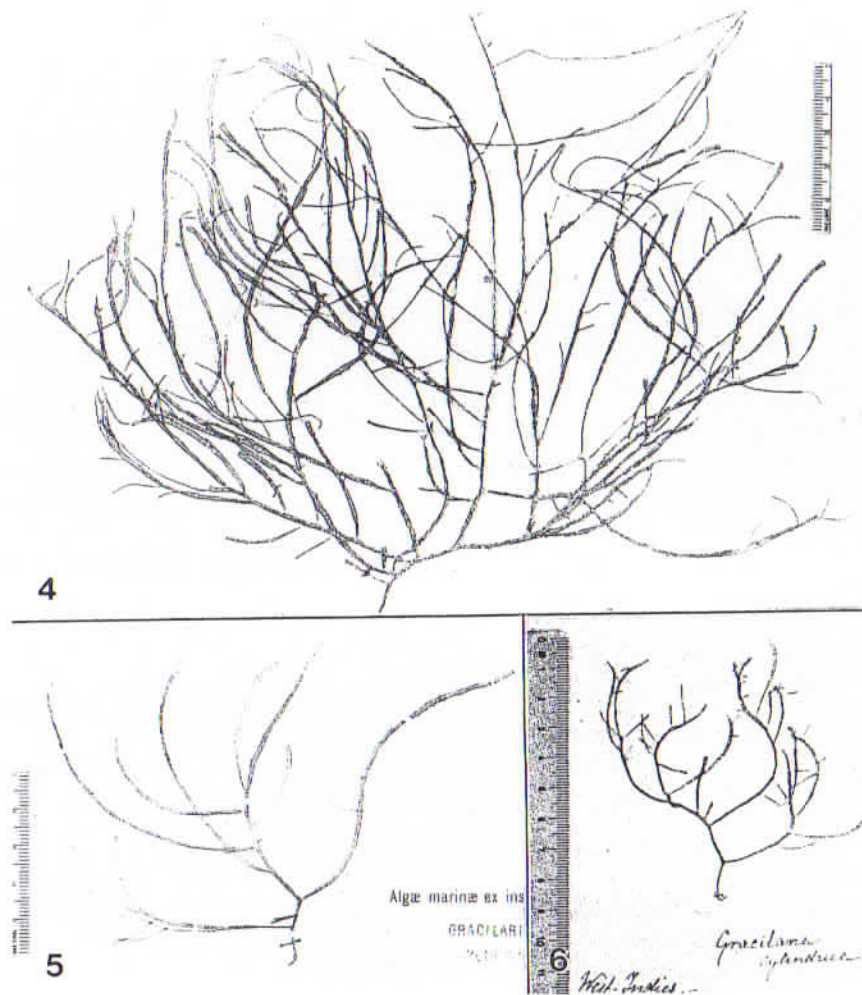
Both taxa are distributed throughout the Caribbean (Taylor 1960), reaching their northernmost distribution in the outer shelf of North Carolina (Schneider and Searles 1973,



Figs. 1-3. *Gracilaria blodgettii*. Fig. 1, Lectotype from Key West, Florida, Blodgett #47 (TCD). Fig. 2, Isotype (TCD). Fig. 3, Isotype (LD, 29309).

Schneider 1975) and southernmost in Guadeloupe (Taylor 1960), with *G. cylindrica* recorded even farther south in Brazil (Joly et al. 1968). Reportedly, they are deep-water species, with *G. blodgettii* dredged from depths of 11 to 36 m and *G. cylindrica* from 15 to 110 m (Taylor 1960). Cheney and Dyer (1974) reported *G. blodgettii* from a depth of 20-60 m in the Florida Middle Ground, off the west coast of Florida in the eastern Gulf of Mexico.

One character commonly used to discriminate species of *Gracilaria* is the type of spermatangial arrangement (Dawson 1949, Yamamoto 1978, Bird and McLachlan 1982). Schneider and Searles (1973) and Reading and Schneider (1986), who used material from the continental shelf off North Carolina, found that the male reproductive apparatus in *G. blodgettii* was organized in shallow pits. Abbott (1988) observed such *textorii*-type spermatangial conceptacles in specimens of *G. cylindrica* from the Virgin Islands.



Figs. 4-6. *Gracilaria cylindrica* Børgesen. Fig. 4, Lectotype from St. Jan, Virgin Islands (C, Børgesen #1973). Fig. 5, Lectoisotype (C, Børgesen #1973). Fig. 6, Syntype (L, Børgesen #1841).

Reports of *G. blodgettii* from outside the Caribbean have been disputed by Abbott et al. (1985). The assignment of this taxon to specimens from China (Zhang and Xia 1984, Xia 1985, Xia and Yamamoto 1985); Japan (Yamamoto 1985), including the Ruykyu Islands (Ohmi 1958, Yamamoto 1978); Taiwan (Chiang 1985); the Philippines (Yamamoto 1989); and Java (Abbott 1988) has been cautioned against and should be reexamined. Abbott (1988) concluded that specimens from Indonesia referred to by Weber van Bosse (1928) as *G. cylindrica*, but bearing *verrucosa*-type conceptacles, belonged instead to a new species and described them as *Polycavernosa vanbosseae* Abbott [= *Hydropuntia vanbosseae* (Abbott) Wynne 1989; *Gracilaria*]. Specimens from Caribbean Panama

referred to as *G. cylindrica* by Hay and Norris (1984) possess distinct *verrucosa*-type conceptacles and represent an undescribed species (personal observations).

Some reports on the amount of tubular nutritive cells within a mature cystocarp have been published. Ortiz Sotomayor (1976) found numerous such cells ("absorbing filaments") linking gonimoblast tissue to pericarp in cystocarps of both *G. blodgettii* and *G. cylindrica* from Puerto Rico. Schneider and Searles (1973) only occasionally saw tubular nutritive cells ("radial trabeculae") in *G. blodgettii* from the North Carolina outer shelf.

Materials and Methods

Specimens fixed in 5% buffered formalin/seawater were stained with aceto-iron-hematoxylin-chloral hydrate (Wittmann 1965) and mounted in 1:1 Hoyer's: water mounting medium according to the procedure of Hommersand and Fredericq (1988). Material not liquid-preserved in formalin was stained and mounted in a mixture of 50% aniline blue/corn syrup (Tsuda and Abbott 1985). Herbarium abbreviations follow Holmgren et al. (1981).

Specimens Examined

Florida: Key West, A. H. Curtiss, *s.n.*, iv.1896, • (NY), and • (US 93064); Dry Tortugas: Southwest Channel, depth 6 fa., 20.vi.26, W. R. Taylor-1383 (NY); off Southwest Channel, dredged 18 fa., 11.vi.25, W. R. Taylor-918 ♂, ♀, and W. R. Taylor-600 • (NY); east of Southwest Channel, dredged 18 fa., 18.vi.26, W. R. Taylor-1429 •, ♀ (NY); 1 mile NNW of Loggerhead Key, dredged 45 fa., 4.vi.25, W. R. Taylor-927 ♀, • (NY); 2.5 mi. NNE of Loggerhead Key, dredged 40 ft., 25.vi.25, W. R. Taylor-991 • (NY).

Virgin Islands: St. Jan: ♀ vic. Annaberg, depth 30 m, 14.iii.06, Børgesen-1973 (C); Cruz Bay, depth 30 m, 29.iii.06, Børgesen-2205 ♀, 24.iii.06, Børgesen-2129 ♂, 8.iii.06, Børgesen-1841 •, ♀, and 5.iii.06, Børgesen-1743 (all C); vic. Cruz Bay, depth 30 m, 23.iii.06, Børgesen-2096 ♀, and 17.iii.06, leg. Dr. Mortensen, Børgesen-2028 ♀ (both C). St. Thomas: M. Hay, January and June 1982, algal plain, 18–36 m, MH-1960 •, MH-1985 ♂, MH-3141, MH-3146 •, MH-3174 •, MH-3163 ♂, MH-3184 ♀, MH-3185 ♀, and MH-3191 ♀ (all US).

Puerto Rico: Off Media Luna Reef, La Parguera, in sand, 28.ii.67, 13–18 m, Almodovar et al. (US 45026); Media Luna Reef, La Parguera, ii.89, Ballantine, *s.n.* ♂, ♀, • (all US); 1.5 km seaward of Media Luna Reef, La Parguera, 17 m (US 95752, 95754, 156536, and 156537), and 2.x.85, Ballantine-2149 (US 95627).

Jamaica: Scots Cove, border St. Elizabeth and Westmoreland, W. R. Taylor (US 60744).

Cuba: Bahía Honda, 7.vi.14, Henderson and Bartsch (US 73583).

Results

Vegetative Growth. Type material of *G. blodgettii* Harvey from Key West, Florida (Figs. 1–3) and of *G. cylindrica* Børgesen from the Virgin Islands (Figs. 4–6) shows that mature thalli of *G. blodgettii* reach an average height of about 10 cm and that those of *G. cylindrica* range from 10 cm to 20 cm. The thalli of both species are single, erect, and attached to the substrate by a discoid holdfast, with branches reaching a width of up to 2 mm. The small type specimens of *G. cylindrica* (Fig. 6) are similar in shape and branching pattern to those of *G. blodgettii* (Fig. 3). The branching pattern in type and type-locality material of these two species is variable, ranging from frequently dense (Figs. 1, 2, 4) to

spare (Figs. 3, 5, 6), and from irregularly alternate (Figs. 1, 2, 4) to a tendency of becoming secund (Figs. 3, 5, 6). Third- and higher-order branches are often beset with short branchlets, 1 mm wide to 3 mm long (Figs. 4, 7, 8). The branchlets of *G. blodgettii* are spindle-shaped or obtuse (Fig. 3), whereas, when present, those of *G. cylindrica* are primarily obtuse (Figs. 5, 6). Although most branches of the second order may not be constricted at their bases, the majority of third- and higher-order branches and branchlets are basally constricted.

Recently collected liquid-preserved material from Puerto Rico shows that the thalli are terete throughout. Branchlets terminate either in spindle-shaped (Figs. 7, 8) or obtuse tips (Fig. 9), and both conditions may exist on a single thallus (Fig. 10). Color is variable, ranging from light pink to crimson-brown. Thalli are relatively coarse (Figs. 7, 9) to slender (Fig. 8). Not cartilaginous in nature, the thalli collapse on drying on herbarium sheets, often disguising their terete nature.

Whereas the transition between cortex and medulla is gradual in young branchlets, it typically becomes abrupt in mature branches, as Harvey depicted in his drawing of a cross section on the herbarium sheet of *G. blodgettii* (Fig. 1). In young branchlets, the medullary cells are multinucleate and rich in cytoplasm, and the terminal cortical cells are anticlinally obovoid. On the other hand, in first- and second-order branches, the pigmented cortex typically consists of one to two layers of cortical cells that become periclinally compressed and a medulla whose cells become hyaline. A cortical cell is generally subtended by a flattened subcortical cell (Figs. 13, 14), and the medulla typically consists of only a few large and irregular roundish cells.

Cortical cells are typically periclinally compressed, uninucleate or multinucleate, reaching a width of 9–15 μm and up to 18 μm long. The average spacing between terminal cortical cells is 5 μm .

Male Reproductive Apparatus. A transection through a male branch from topotypic material of *G. blodgettii* and type material of *G. cylindrica* reveals that spermatangial parent cells and their spermatangia are organized into very shallow spermatangial sori, i.e., *textorii*-type sensu Yamamoto (1978). They are also seen in Figs. 15, 16.

In material of *G. blodgettii* from Puerto Rico (Figs. 17, 18), two different focal views seen from the surface of a second-order male branch indicate that the spermatangia are organized into broadly ellipsoid patches or sori that reach an average length of 25 μm and a width of 20 μm (Figs. 11, 12). The spermatangia (Fig. 11) are at the level of the terminal undifferentiated cortical cells; the spermatangial parent cells, linked to one another by primary pit connections, are at the level of the subcortical/medullary cells (Fig. 12). In a transverse section, each male sorus that has reached full maturity has an average depth of 12–18 μm and consists of 12–20 spermatangial parent cells.

The sequential development begins with a generative outer cortical cell producing a series of spermatangial parent cells that lead to the establishment of a spermatangial sorus (Figs. 19–40 and accompanying diagrams 19–38). The last diagram for each figure number reflects the situation as seen in the photograph. For each number, the diagram or diagrams in front of the last diagram show the most likely hypothetical developmental pathway. Tracing back the pit connections on a cell-by-cell basis gives a reliable indication of how the spermatangial parent cells were previously cut off. The diagrams do not take into account size, shape, or plane of orientation of the spermatangial parent cells.

First, an outer cortical cell divides by an anticlinal concavo-convex division into a pair of spermatangial parent cells (Figs. 19, 20). This generative outer cortical cell is commonly the only cell subtended by a periclinally compressed larger subcortical cell (Fig.



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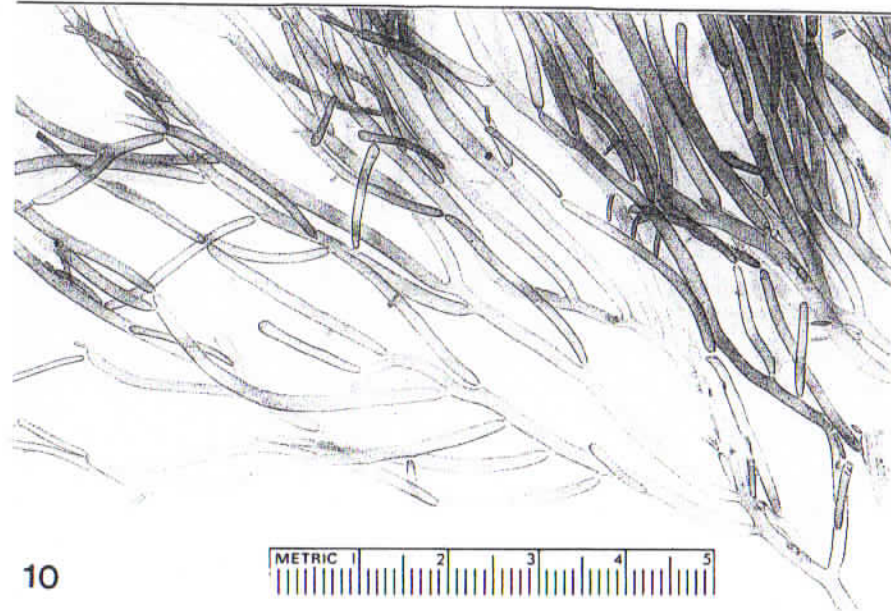


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Figs. 7, 8. *Gracilaria blodgettii* from Puerto Rico (liquid-preserved). Fig. 7, female specimen (US 156536) showing discoid holdfast (arrowhead), with majority of third- and higher-order branches and branchlets basally constricted. Fig. 8, Slender, small male specimen (US 156537) with majority of third- and higher-order branches and branchlets basally constricted.

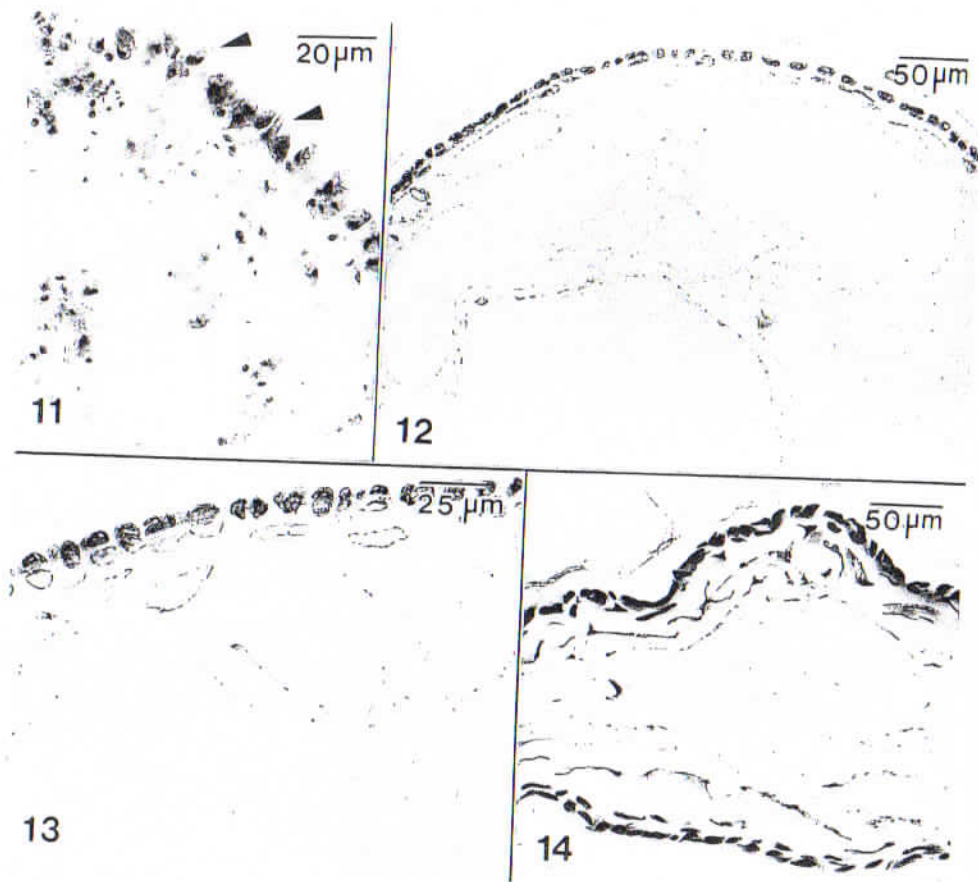


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Figs. 9, 10. *Gracilaria "cylindrica"* from Puerto Rico (liquid-preserved). Fig. 9, specimen (US 95752) with majority of third-order branches and branchlets basally constricted. Fig. 10, Close-up of Fig. 9, showing obtuse or spindle-shaped branchlet tips.



Figs. 11–13. Vegetative morphology of *Gracilaria blodgettii* from Puerto Rico (US 95754). Fig. 11, Transverse section through young branchlet showing multinucleate medullary cells and anticlinally obovoid terminal cortical cells (arrowheads). Fig. 12, Transverse section through a first-order branch showing vacuolate, large-celled medulla and one- to two-celled cortex (aniline blue). Fig. 13, Transverse section through a second-order branch (aniline blue). Fig. 14, Transverse section through second-order branch in lectotype specimen of *Gracilaria cylindrica* (C, Børgesen #1973; aniline blue).

19). Occasionally, a subcortical cell subtends more than one outer cortical cell, which may (Fig. 27) or may not (Figs. 20, 26) become generative. The parent cell initial, connected by a primary pit connection to its subcortical cell, then divides in a plane different from the first one, leading to three spermatangial parent cells (Fig. 21). As soon as three spermatangial parent cells are established, each may cut off a single, colorless, uninucleate spermatangium by a concavo-convex septum (Fig. 22). One of the parent cells then divides further at either oblique or straight angles, leading to four (Figs. 23–25, 27) spermatangial parent cells. It is common that at the four-cell stage no spermatangia have yet been initiated (Figs. 23–25, 27). A subcortical cell occasionally bears two sets of

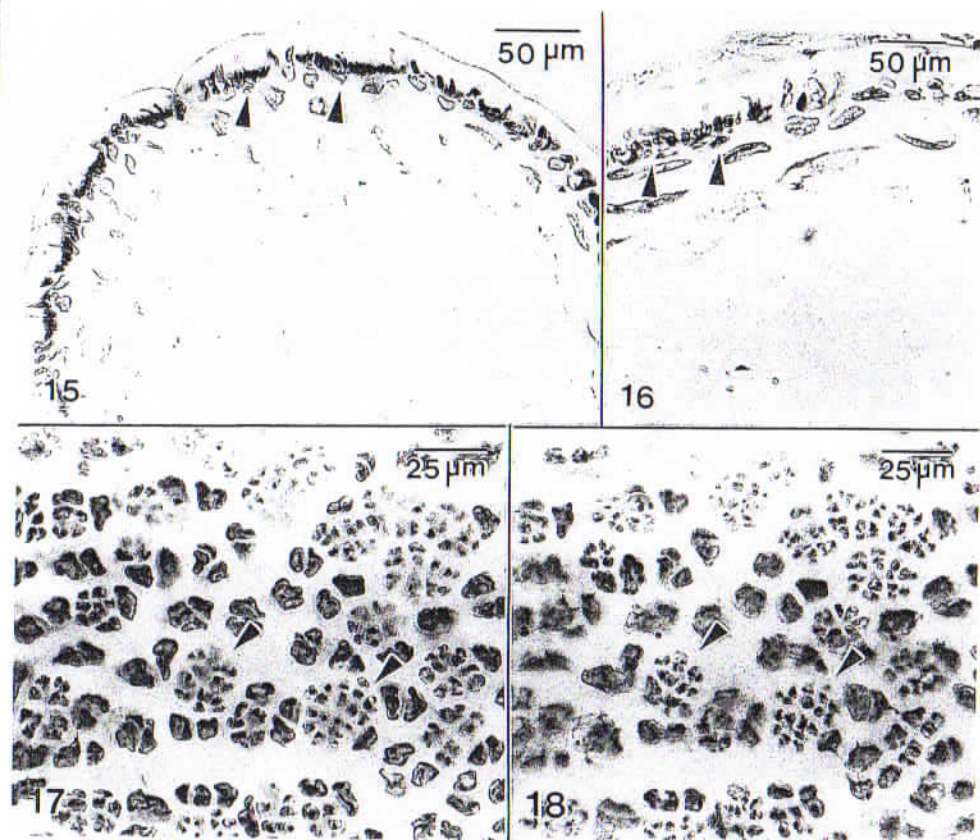


Fig. 15. Transverse section of male specimen of *Gracilaria blodgettii* from Dry Tortugas, Florida (NY, W. R. Taylor #918), showing shallow spermatangial sori (arrowheads; aniline blue).

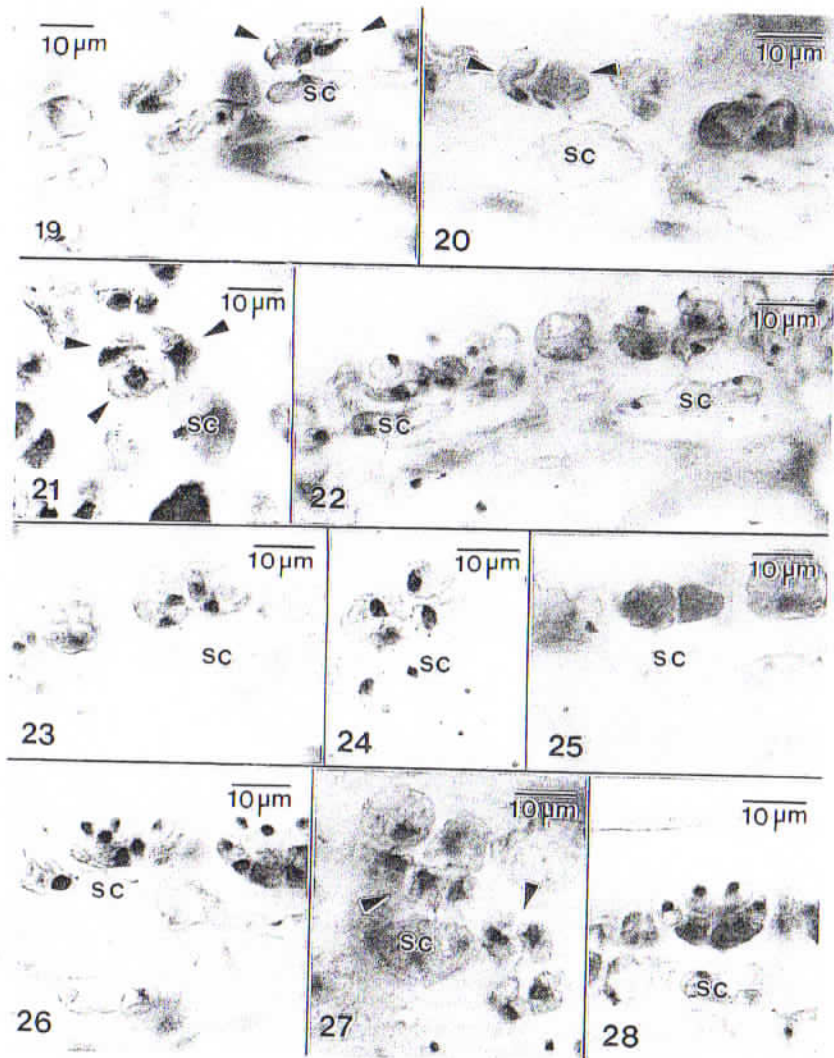
Fig. 16. Transverse section of a male syntype specimen of *Gracilaria cylindrica* (C, Børgesen #2129) showing spermatangial sori (arrowheads; aniline blue).

Figs. 17, 18. Two different focal planes showing surface view of spermatangial sori of *G. blodgettii* from Puerto Rico (US 156537). Fig. 17, at level of spermatangia (arrowheads); Fig. 18, at level of spermatangial parent cells (arrowheads).

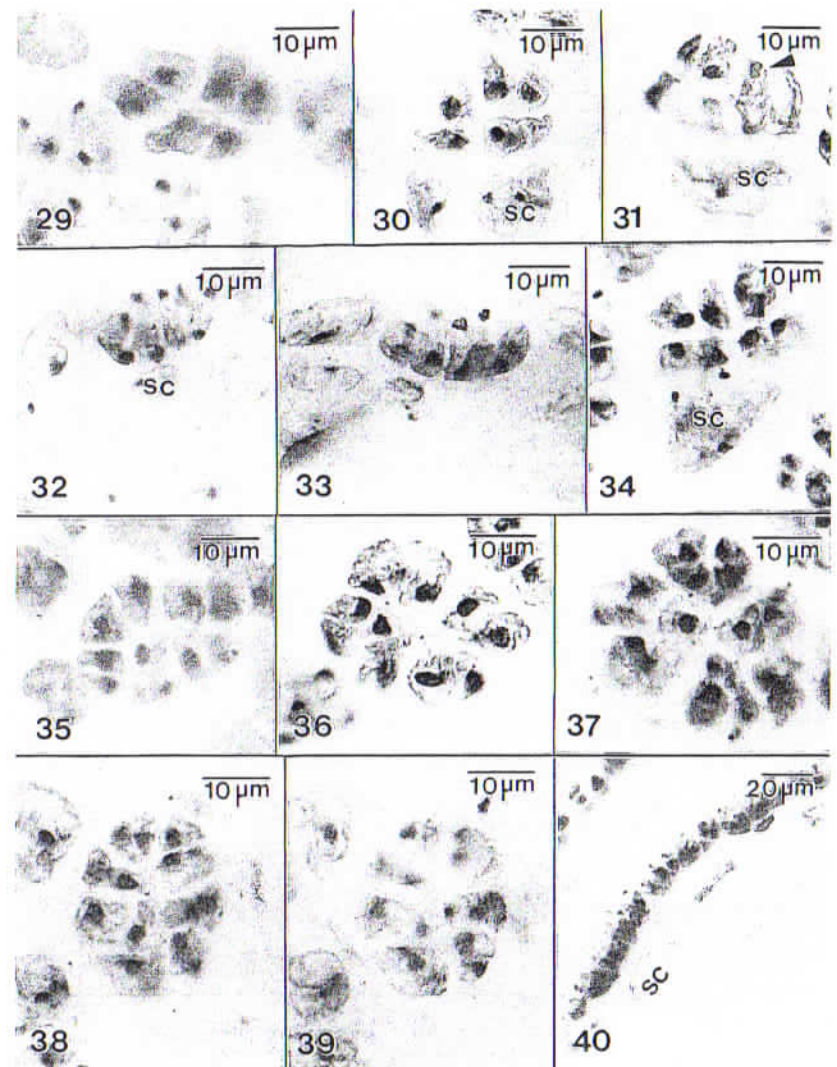
spermatangial parent cells (Fig. 27), indicating that both the outer cortical cells became generative.

At the five-cell stage, a small and shallow male sorus is recognizable, in which each spermatangial parent cell has cut off a spermatangium (Fig. 28). When a pit connection is seen between the central spermatangial parent cell (which is the spermatangial parent cell initial) in a transverse section, it indicates that the section cut straight through the center of the young male sorus. When such a pit connection is absent, the section went instead through the marginal spermatangial parent cells.

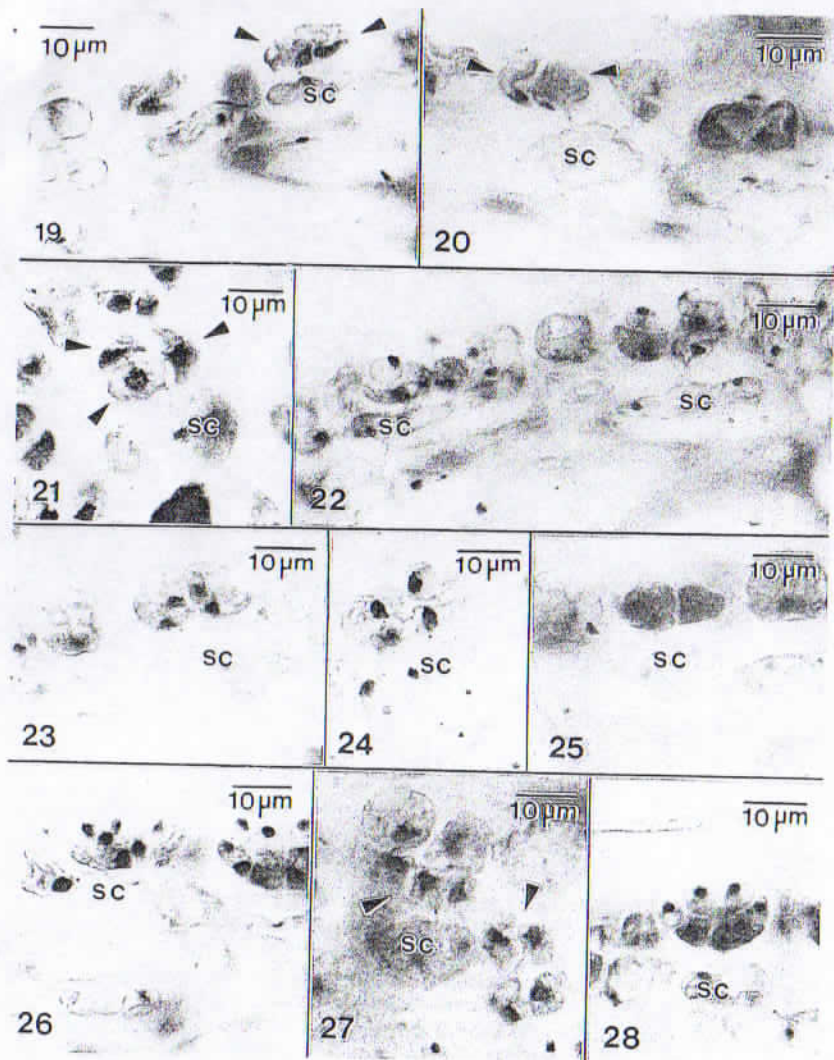
A surface view shows that a spermatangial sorus becomes ellipsoid when six to eight



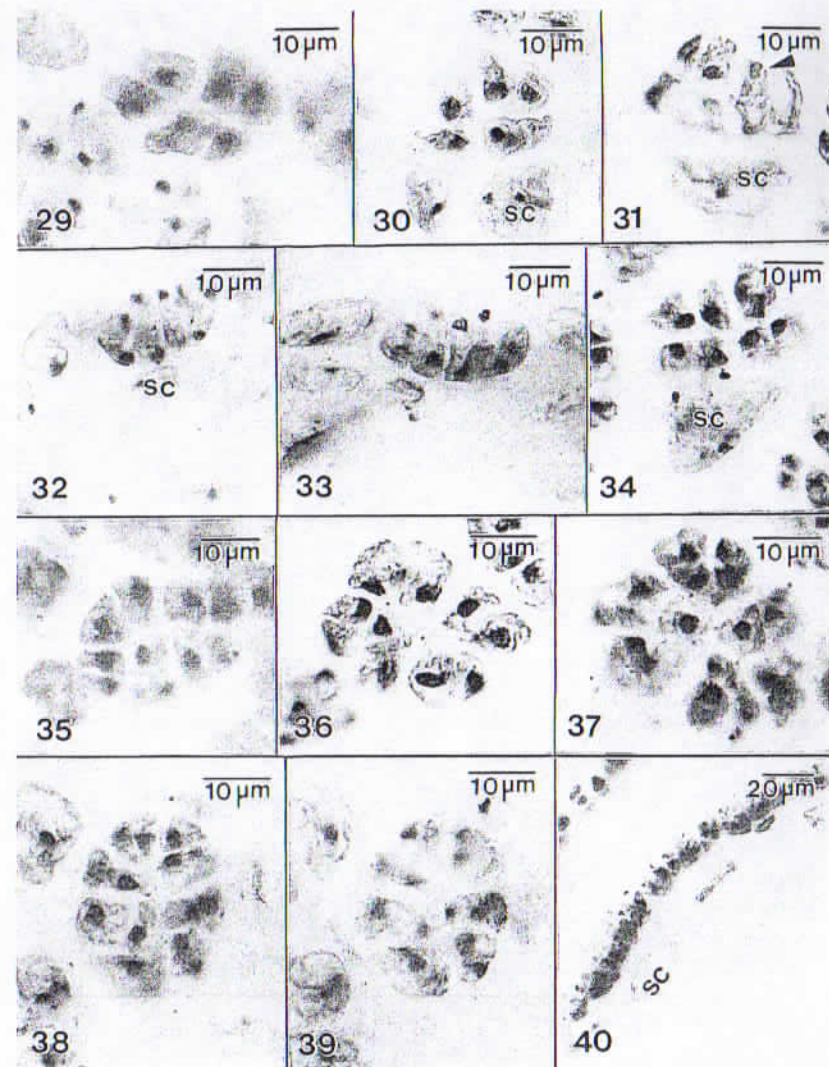
Figs. 19–28 and diagrams 19–28. See text for explanation of diagrams. Spermatangial *Gracilaria blodgettii* from Puerto Rico (US 156537). Development of spermatangial parent cells into spermatangial sori. sc = subcortical cell. Figs. 19, 20, Outer cortical cell divided into pair of spermatangial parent cells (arrowheads; surface squash). Fig. 21, Three spermatangial parent cells (arrowheads; surface squash). Fig. 22, At left and right: three spermatangial parent cells (arrowheads), with spermatangia in focus (transverse section). Figs. 23–25, Four spermatangial parent cells (transverse section). Fig. 26, Four spermatangial parent cells, each with a spermatangium (transverse section). Fig. 27, Subcortical cell bearing two sets of spermatangial parent cells (arrowheads), five at left and four at right (surface squash). Fig. 28, Five spermatangial parent cells, each with a spermatangium (transverse section).



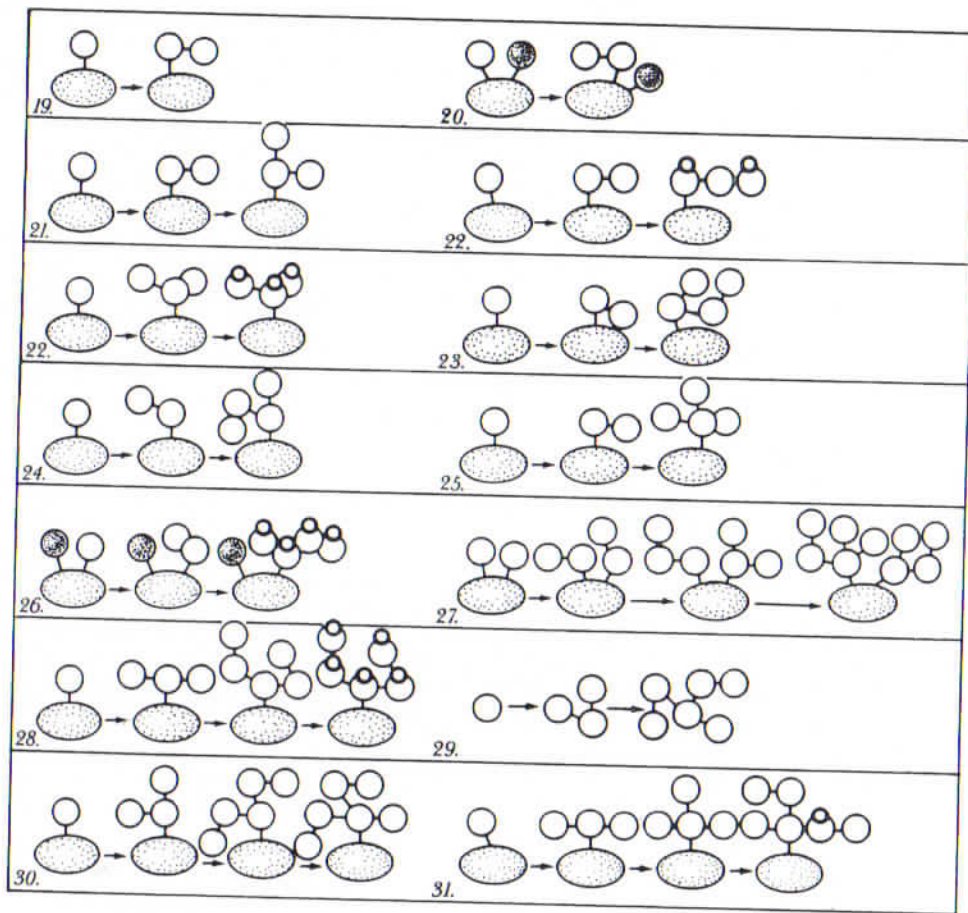
Figs. 29–40 and diagrams 29–38. See text for explanation of diagrams. Spermatangial *Gracilaria blodgettii* from Puerto Rico (US 156537), showing development of spermatangial parent cells into sori. sc = subcortical cell. Figs. 29, 30, Six spermatangial parent cells (surface squash). Fig. 31, Six spermatangial parent cells with one spermatangium (arrowhead) in focus (surface squash). Figs. 32, 33, Six spermatangial parent cells, each with spermatangium (transverse section). Fig. 34, Eight spermatangial parent cells (surface squash). Fig. 35, Ten spermatangial parent cells (surface squash). Fig. 36, Eleven spermatangial parent cells (surface squash). Fig. 37, Fourteen spermatangial parent cells (surface squash). Figs. 38, 39, Two different focal planes showing a spermatangial sorus containing 12 spermatangial parent cells (surface squash): Fig. 38, at level of parent cells; Fig. 39, at level of spermatangia. Fig. 40, Transverse section through mature spermatangial cortex.



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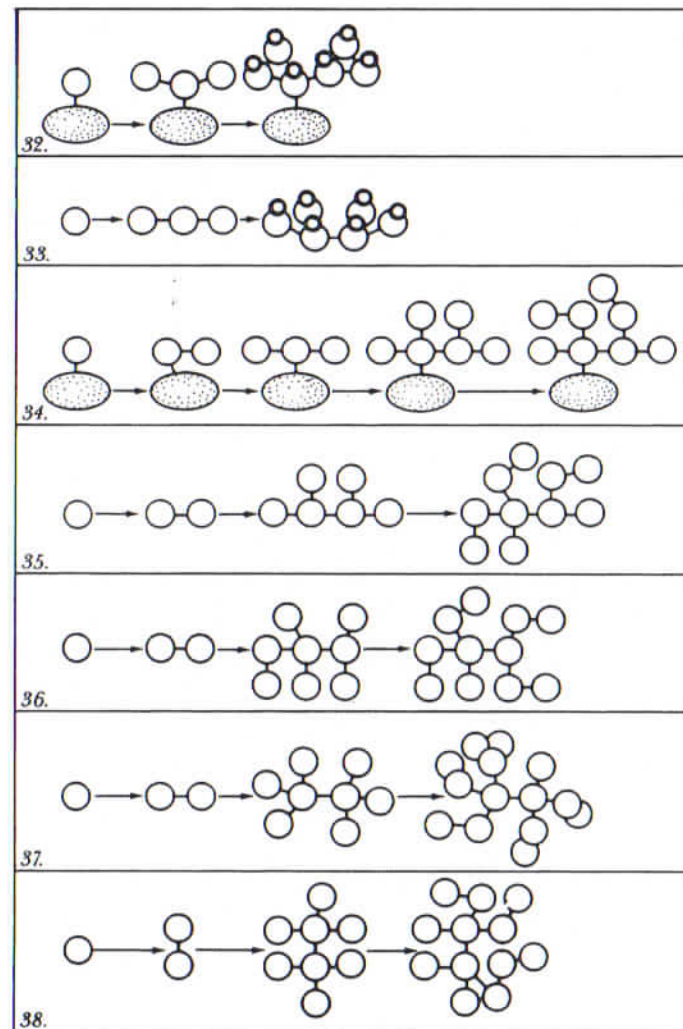


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- Spermatangium
- Spermatangial parent cell
- Unidentified cortical cell
- ◐ Subcortical cell

See text and caption for figures 19–38.



spermatangial parent cells cut off sequentially become organized in two cell rows (Figs. 29–31, 34). Whereas surface views of young sori show exclusively on either the spermatangial parent cells or the spermatangia, a transverse section representing the equivalent developmental stage reveals both types of cells (Figs. 32, 33).

When 10 spermatangial parent cells have been cut off, the sorus becomes three cells wide or more (Figs. 35–39). A sorus of up to 14 spermatangial parent cells (Fig. 37) can be readily distinguished on a cell-by-cell basis, but a sorus may consist of up to 20 such parent cells. A view of a male sorus at the level of spermatangia (Fig. 39) shows that the spermatangia develop centripetally within a sorus. Occasionally in a mature spermatangial cortex (Fig. 40), neighboring sori are continuous instead of being interspersed among undifferentiated vegetative cells.

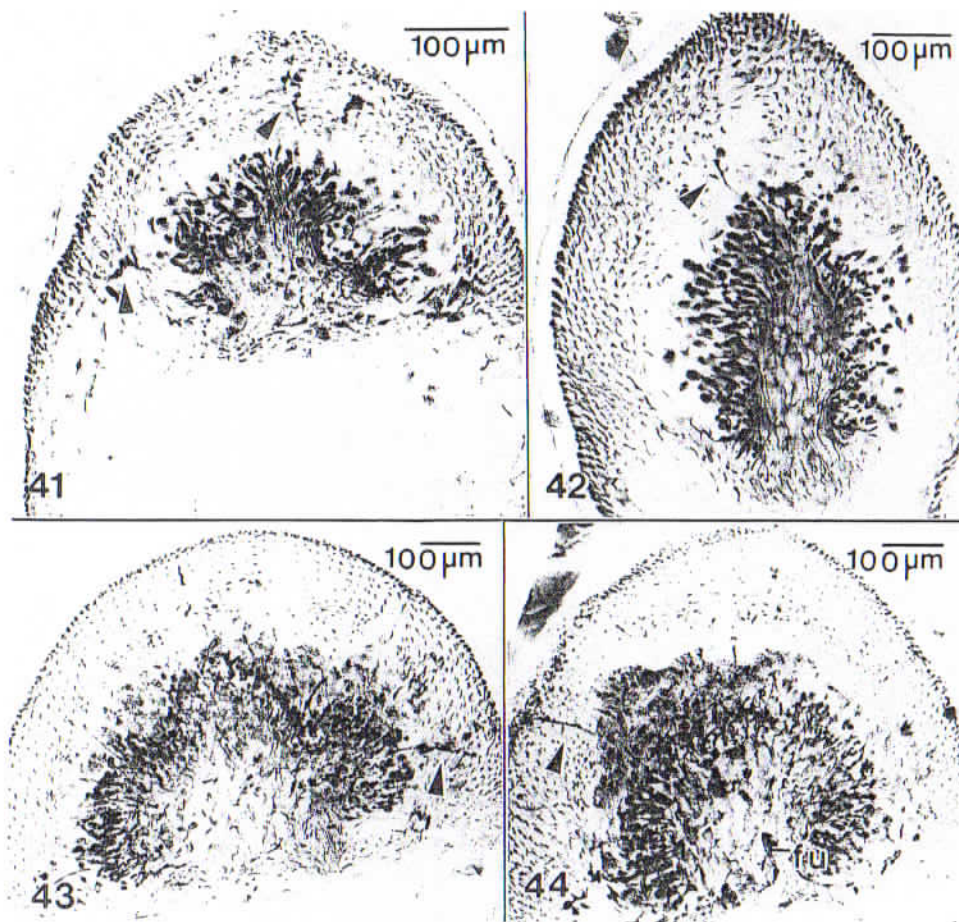
Cystocarp Development. Transverse sections through mature cystocarps in topotypic material of *G. blodgettii* (Figs. 41, 42) and type material of *G. cylindrica* (Figs. 43, 44) reveal that both possess a sterile gonimoblast that bears tubular nutritive cells that reach a well-developed pericarp of 10–15 cell layers. A globose fusion cell also persists (Fig. 44).

Unfertilized carpogonial branches were not available in the material examined. After fertilization, the multinucleate fusion cell cuts off small, roundish, uninucleate gonimoblast cells and typically becomes globose distally (Fig. 45). The lowermost part of the fusion cell incorporates, laterally around pit connections, multinucleate neighboring vegetative cells for a distance of up to three cortical cell files (Figs. 45, 46). On further division of the uninucleate gonimoblast cells, the gonimoblast cells form pit connections with the fusion cell (Fig. 47), and the lowermost gonimoblast cells (Fig. 49) expand in size and become multinucleate. These multinucleate gonimoblast cells bear distally small clusters of uninucleate gonimoblast cells while issuing, at their lower side, multinucleate, tubular nutritive cells (Figs. 47–49) toward the pericarp. At this stage, the multinucleate gonimoblast cells have not yet formed secondary pit connections with neighboring cells, and thus a sterile gonimoblast has not yet developed (Fig. 48).

While the divisions of gonimoblast cells continue laterally and upward in such young cystocarps, the tubular nutritive cells increase in length, with their tips fusing directly onto pericarp cells (Fig. 50). Distal uninucleate gonimoblast cells do not increase in size (Fig. 51) until they become transformed into carposporangial initials. The transition from gonimoblast cell into carposporangial initial comes about by their gradual enlargement (Fig. 52). Inner gonimoblast cells that are not transformed into carposporangial initials make up the sterile gonimoblast (Fig. 53). Further maturation of the cystocarp follows the same pattern as in young cystocarps; the only difference is a gradual incorporation of a greater number of inner gonimoblast cells into a vacuolate sterile gonimoblast and a large number of carposporangia (Figs. 54, 55) in the mature condition.

Carposporangial chains distal to the sterile gonimoblast can reach a length of up to six cells (Figs. 56, 57). The basal-most initials commonly are rectangular, reaching a width of up to 9 μm before expansion (Fig. 57). Carposporangia are usually obovate in side view and roundish in top view, and may be up to 45 μm long and 35 μm wide.

Mature cystocarps (Figs. 58–60) typically consist of a persisting fusion cell, even after the formation of carposporangia, sterile gonimoblast, tubular nutritive cells, and a pericarp with a central ostiole (Fig. 60). Tubular nutritive cells (Figs. 58–60) in the material examined were fusing abundantly with pericarp cells. The pericarp consists of 10–15 layers of squarish/roundish cells organized in anticlinal rows (Fig. 61).

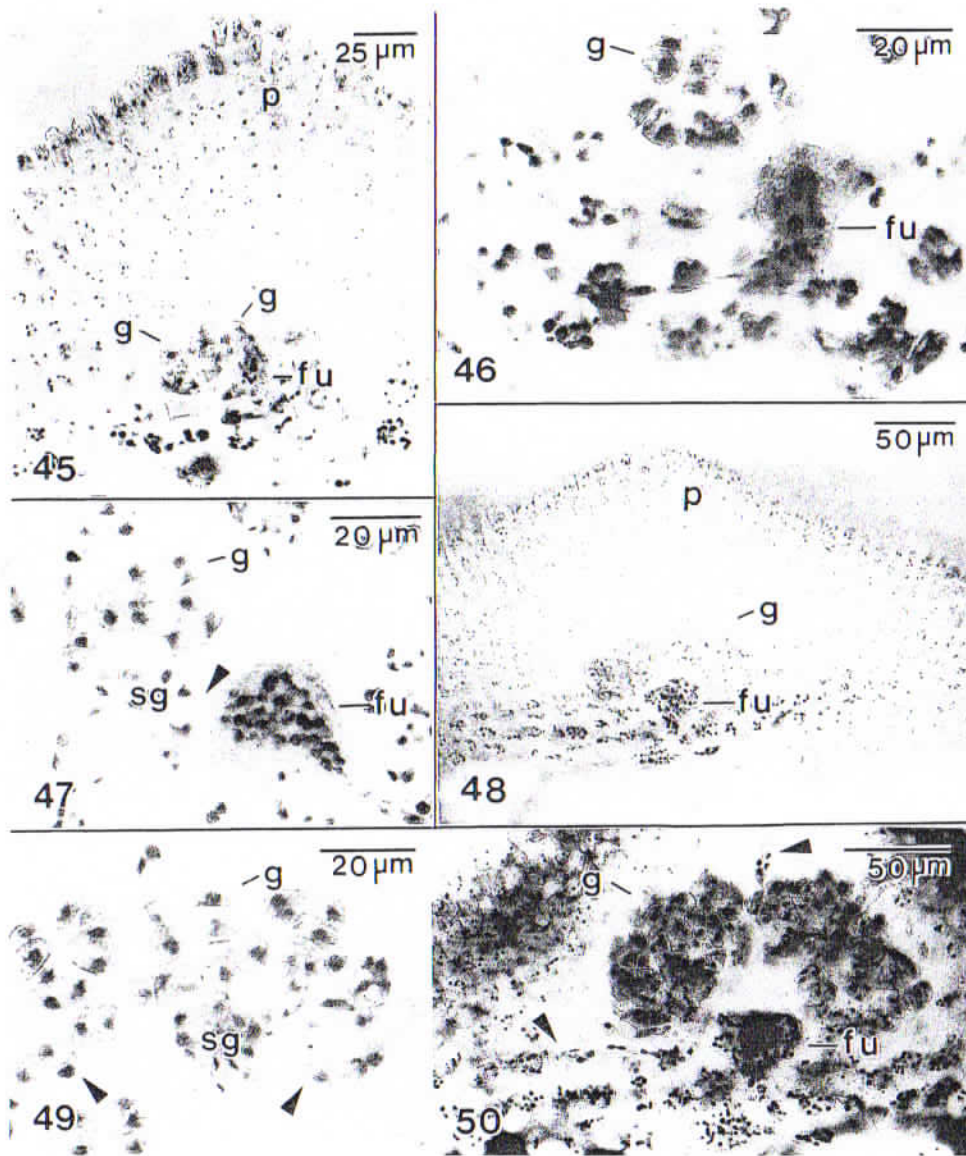


Figs. 41–44. Transverse sections through mature cystocarp showing tubular nutritive cells (arrowheads; aniline blue). Figs. 41, 42, *Gracilaria blodgettii* from Dry Tortugas, Florida (NY, Taylor #918). Fig. 43, Lectotype of *Gracilaria cylindrica* (C. Børgesen #1973). Fig. 44, Cystocarp from lectotype of *G. cylindrica* (C. Børgesen #1973) showing a globose fusion cell (fu).

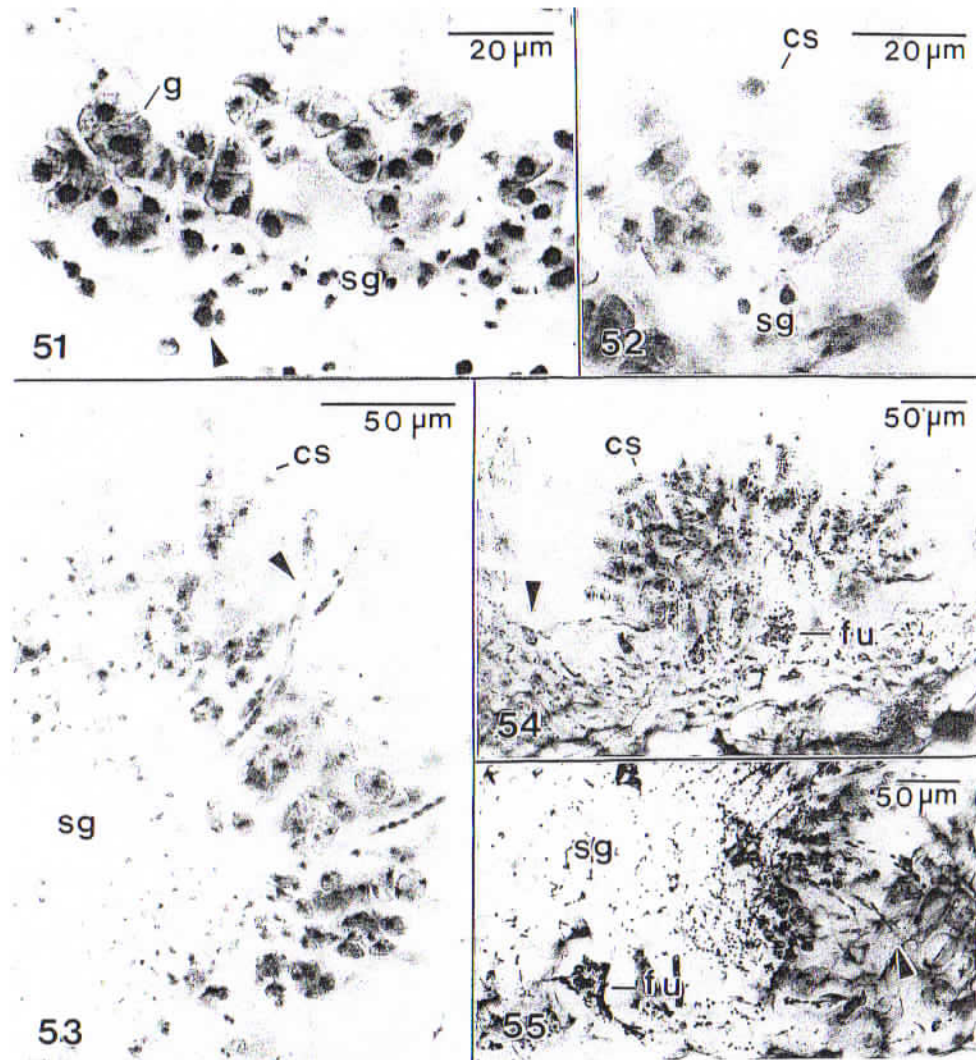
Cystocarps are generally abundant and scattered over the surfaces of second- and third-order branches of a female thallus. Hemispherical and urceolate to globose, cystocarps project considerably from the thallus, are up to 1.5 mm in diameter and 2.0 mm tall, and are not constricted at the base.

Discussion

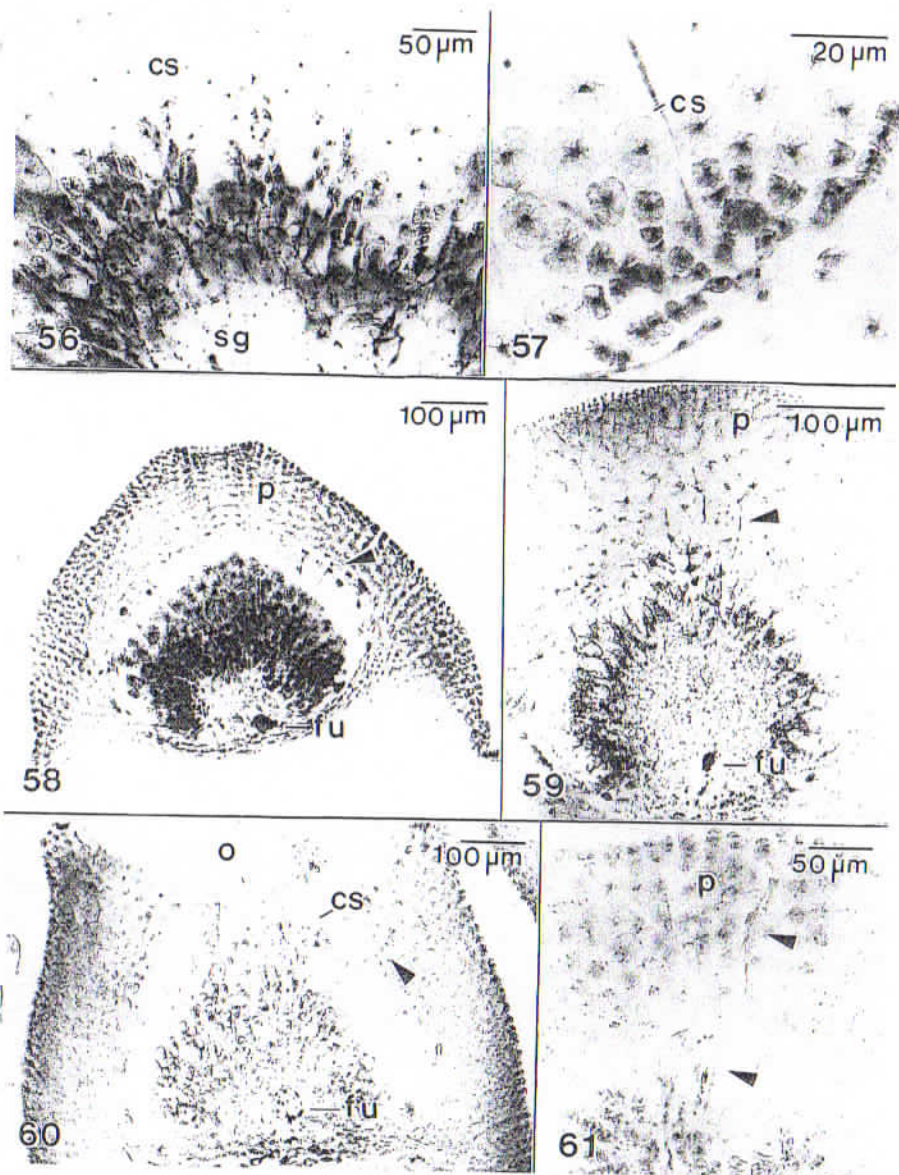
Of great interest are the new findings on the development of the male reproductive



Figs. 45–50. *Gracilaria blodgettii* from Puerto Rico (US 156536), showing stages of postfertilization development. fu = fusion cell, g = gonimoblasts, p = pericarp, sg = lower or sterile gonimoblast cell. Fig. 45, Young cystocarp with fusion cell, gonimoblasts (arrowheads), and pericarp. Fig. 46, Multinucleate fusion cell with small cluster of gonimoblast cells. Fig. 47, Uninucleate gonimoblast cells; lower gonimoblast cell with pit connection (arrowhead) to fusion cell has become multinucleate. Fig. 48, Young cystocarp before initiation of sterile gonimoblast. Fig. 49, Lower gonimoblast cells with young files of uninucleate gonimoblast cells distally, and multinucleate tubular nutritive cells proximally (arrowheads). Fig. 50, Cystocarp with tubular nutritive cells (arrowheads).



Figs. 51–55. *Gracilaria blodgettii* from Puerto Rico (US 156536) showing stages of postfertilization development. cs = carposporangia, fu = fusion cell, p = pericarp, sg = lower or sterile gonimoblast cell. Fig. 51, Lower gonimoblast cell bearing cluster of uninucleate gonimoblast cells distally and tubular nutritive cells proximally (arrowheads). Fig. 52, Initiation of carposporangia. Fig. 53, Sterile gonimoblast, carposporangia, and elongate tubular nutritive cells (arrowheads). Figs. 54, 55, Cystocarp with fusion cell and tubular nutritive cell fusing (arrowhead) with pericarp cell.



Figs. 56–61. *Gracilaria blodgettii* from Puerto Rico (US 156536) showing stages of postfertilization development. cs = carposporangia, fu = fusion cell, o = ostiole, p = pericarp, sg = sterile gonimoblast cell. Fig. 56, Sterile gonimoblast with rather straight clusters of carposporangia. Fig. 57, Chains of carposporangia. Fig. 58, Mature cystocarp with tubular nutritive cells (arrowheads; aniline blue). Fig. 59, Mature cystocarp with tubular nutritive cells (arrowheads). Fig. 60, Mature cystocarp with ostiole in pericarp. Fig. 61, Tubular nutritive cells (arrowheads) reaching the pericarp.

apparatus in *G. blodgettii*. Compared with other Caribbean species with *textorii*-type male configuration, such as *G. cervicornis* (Turner) J. Agardh (Oliveira et al. 1983), the sori of *G. blodgettii* Harvey (including *G. cylindrica* Børgesen) that we examined are markedly uniformly shallow, a condition Reading and Schneider (1986) found in material they identified as this species from the outer continental shelf off North Carolina. This shallowness seemingly results because the marginal spermatangial parent cells within each sorus grow only slightly acropetally in relation to the central ones and do not cut off more derivative parent cells beyond the 20-cell stage. The compactness of terminal cortical cells also seems to be a limiting factor determining sorus width; the wide spacing between individual outer cortical cells in *G. blodgettii* could thus also allow the establishment of relatively wide sori. The number of spermatangial parent cells within a sorus may be fixed for each species, and potentially may be a character of taxonomic importance.

Because a subcortical cell commonly subtends only a single terminal cortical cell in *G. blodgettii*, the shallow sori in this species frequently appear to be continuous over entire patches on the male branches. This shallow *textorii*-type configuration may be mistaken for the superficial *chorda*-type configuration inherent to species belonging to *Gracilariopsis* Dawson (e.g., Dawson 1949, Fredericq and Hommersand 1989b). In *Gracilariopsis*, however, both spermatangial parent cells result from division of an outer cortical cell and are restricted to a pair or group of three by concavo-convex longitudinal divisions. Further, each spermatangial parent cell cuts off only a single spermatangium by a transverse division (Fredericq and Hommersand 1989b).

The *textorii*-type sorus of *G. blodgettii* clearly differs in size from *verrucosa*-type configuration of *G. verrucosa* (Hudson) Papenfuss, the type species of *Gracilaria* Greville (e.g., Yamamoto 1978, Fredericq and Hommersand 1989a). In *G. verrucosa*, the spermatangial parent cells are generated in extensive filaments from intercalary cortical cells that line an intercellular space forming a much deeper "conceptacle" (Fredericq and Hommersand 1989a). Because the spermatangial parent-cell primordia in *G. blodgettii* are ordinary terminal rather than intercalary cortical cells as in *G. verrucosa*, and because both taxa generate spermatangia by a concavo-convex septum, it seems that both types of cortical cell may function as spermatangial parent cell primordia and are thus found within the genus *Gracilaria*.

Conclusion

Whether there are two species has been in question almost since Børgesen (1920) described *G. cylindrica*. For example, Taylor (1960) remarked that some shallow-water specimens were perhaps intermediate between *G. cylindrica* and *G. blodgettii* in the western Atlantic, "but usually the two species are easily distinguished," and Bird et al. (1987), using data from analytical pyrolysis of herbarium material, suggested "a concrete difference between these two entities." However, in our studies of recent collections, whose identity was based on comparative studies of type specimens and topotypic material, we found no inherent differences to support treating *G. blodgettii* Harvey and *G. cylindrica* Børgesen as two distinct taxa.

Therefore, in the western Atlantic, both coarse and slender terete specimens that possess basally constricted third- and higher-order branches and branchlets, spindle-shaped and obtuse branchlets on a single thallus, a medulla of a few large cells, a cortex of one to two cell layers, very shallow *textorii*-type male sori, and cystocarps with

numerous tubular nutritive cells linking gonimoblast with pericarp should be referred to as a single species as follows: *Gracilaria blodgettii* Harvey (Harvey 1853, p. 111) LT: TCD = *Gracilaria cylindrica* Børgesen (Børgesen 1920, p. 375, figs. 364–365) LT: C.

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