

## A MORPHOLOGICAL STUDY AND TAXONOMIC REASSESSMENT OF THE GENERITYPE SPECIES IN THE GRACILARIACEAE<sup>1</sup>

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**We investigated the reproductive morphology of representative material corresponding to the type species of each of the described genera presently placed in synonymy under *Gracilaria*. From these observations and published studies of recognized genera, 10 species groups are identified in the Gracilariaceae based on spermatangial type and cystocarp development. Actual or potential generic names are given in brackets after each group: 1) abscissa group (*Melanthalia*), 2) flabellata group (*Curdiea*), 3) lemaneiformis group (*Gracilariopsis*), 4) chilensis group, 5) edulis group (*Plocaria*/*Polycavernosa*), 6) urvillei group (*Hydropuntia*), 7) crassissima group, 8) salicornia group (*Corallopsis*), 9) gracilis group, and 10) bursa-pastoris group (*Gracilaria*). *Tyleiophora* was shown to belong to the bursa-pastoris group. The type species of the parasitic genera *Gracilariophila* and *Congracilaria* are closely related to their host species. Species assemblages recognized here based on morphological evidence received moderate to strong bootstrap support in recently published molecular phylogenies. Further studies may show that some groups correspond to genera, whereas others do not merit generic status.**

**Key index words:** cystocarp; Gracilariaceae; Gracilariales; marine algae; morphology; Rhodophyta; taxonomy

The Gracilariaceae was established as Gracilariaceae by Nägeli (1847, pp. 240, 254) and redefined by Kylin (1932, p. 57) based on features of cystocarp development as described in Sjöstedt (1926) and Kylin (1930). Kylin (1956) recognized eight genera in the Gracilariaceae: *Gracilaria* Greville (1830, including *Cordylecladia* J. Agardh [1852]), *Corallopsis* Greville (1830, including *Hydropuntia* Montagne [1842]), *Melanthalia* Montagne (1843), *Tyleiophora* J. Agardh (1890, incorrectly as *Tylotus* J. Agardh [1876]), *Curdiea* Harvey (1855b, including *Sarcocladia* Harvey [1855a]), *Gelidiopsis* Schmitz (1895), *Ceratodictyon* Zanardini (1878), and *Gracilariophila* Setchell et Wilson in Wilson (1910). *Cordylecladia*, *Gelidiopsis*, and *Ceratodictyon* have since been removed to the Rhodymeniales (Brodie and Guiry 1988, Price and Kraft 1991). Kylin treated the *Gracilariocolax* Weber-van Bosse (1928) as a parasitic

genus of uncertain position. Two names have been rejected against *Gracilaria* Greville (1830, nom. cons.): *Ceramianthemum* Donati ex S. Léman (1817) and *Plocaria* Nees (1820) (Silva 1952, Silva in Farr et al. 1979). Genera proposed since Kylin include *Gracilariopsis* Dawson (1949), *Polycavernosa* Chang et Xia (1963), and *Congracilaria* Yamamoto (1986). *Gracilariopsis* was placed in synonymy under *Gracilaria* by Papenfuss (1967) and later reinstated by Fredericq and Hommersand (1989b). *Hydropuntia* was reinstated by Wynne (1989) to include *Polycavernosa*. This name has been accepted by some authors and rejected by others.

Except for the largely Australasian genera *Melanthalia* and *Curdiea* and the parasitic genera *Gracilariophila*, *Gracilariocolax*, and *Congracilaria*, virtually all species belonging to the Gracilariaceae have been placed in *Gracilaria* at one time or another. In the absence of defining characters that might serve to separate genera, most workers have followed Bird et al. (1992) and Abbott (1995) in maintaining species that might be confused at the generic level in *Gracilaria*. This opinion of respected authorities places the burden of proof on any worker who should propose splitting up the genus. On the other hand, it is unlikely that the Gracilariaceae, with 100–200 species that are widely distributed throughout the temperate and tropical regions of the world, have not diverged into taxa that could be recognized at the generic level. Morphological and phylogenetic studies have reached a point where the balance of opinion is likely to shift away from a single genus concept to a classification that recognizes several genera.

Anticipating this change of opinion, we investigated the reproductive morphology of representative material corresponding to the type species of all the described genera currently placed in synonymy under *Gracilaria* in the expectation that some of the names may ultimately gain acceptance, whereas others remain synonymous with *Gracilaria*. The following are the available generic names and the present placement of the nonparasitic type species in *Gracilaria* and the parasitic genera listed in their order of priority: *Gracilaria* Greville (1830, nom. cons.), type species *Gracilaria compressa* (C. Agardh) Greville (= *G. bursa-pastoris* [S. G. Gmelin] P. C. Silva [1952]; see Steentoft et al. 1991); *Ceramianthemum* Donati ex S. Léman (1817) (= *Ceramion* Adanson [1763, nom. rej.]), type species, *Ceramianthemum ramosissimum*, *humile*, *pellucidum*, *rubrum* Donati (1753) (= *G. bursa-pastoris* [S. G. Gmelin] P. C. Silva [1952]); *Plocaria* Nees (1820), type species *Plocaria candida* Nees (= *G. edulis* [S. G. Gmelin]

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P. C. Silva [1952]); *Corallopsis* Greville (1830), type species *Corallopsis salicornia* (C. Agardh) Greville (= *G. salicornia* [C. Agardh] Dawson [1954]); *Hydropuntia* Montagne (1842), type species *Hydropuntia urvillei* Montagne (= *G. urvillei* [Montagne] Abbott in Abbott et al. [1991]); *Tyleiophora* J. Agardh (1890), type species *Tyleiophora beckeri* J. Agardh (= *G. beckeri* [J. Agardh] Papenfuss [1952]); *Gracilariophila* Setchell et Wilson in Wilson (1910), type species *Gracilariophila oryzoides* Setchell et Wilson in Wilson (1910); *Gracilariocolax* Weber-van Bosse (1928), type species *Gracilariocolax henriettae* Weber-van Bosse (1922); *Gracilariopsis* Dawson (1949), type species *Gracilariopsis sjoestedtii* (Kyllin) Dawson (= *Gracilariopsis andersonii* [Grunow in Piccone] Liao et Hommersand in Gurgel et al. [2003]); *Polycavernosa* Chang et Xia (1963), type species *Polycavernosa fastigiata* Chang et Xia (= *G. edulis* [S. G. Gmelin] P. C. Silva [1952]; see Abbott et al. 1991); and *Congracilaria* Yamamoto (1986), type species *Congracilaria babae* Yamamoto (1986). We examined formalin-fixed material of *Gracilaria eucheumatoides* Harvey (1860), for comparison with herbarium specimens of *G. urvillei*, and *Gracilaria aculeata* (Hering) Papenfuss (1967), an unusual species related to *G. salicornia*, to illustrate similarities and differences between the two. *Gracilaria chilensis* Bird, McLachlan et Oliveira (1986) is covered briefly to document a critical stage in cystocarp development. We analyzed the comparative morphology of spermatangial and cystocarpic features and provided a table of diagnostic characters and a discussion of species complexes in the Gracilariaceae based on previously published studies and our own observations.

#### MATERIALS AND METHODS

Specific information on collections examined here is given in the Results section. Materials were collected and preserved in 10% formalin-seawater and left for at least 24 h before transfer to 5% formalin-seawater for preservation. Before sectioning, samples were bleached under a lamp for at least 24 h to destroy pigments that might interfere with the staining reaction. Bleached samples were heat dried to a desired firmness and hand sectioned with a double-edged platinum-chrome razor blade, rehydrated and stained with aceto-iron-hematoxylin-chloral hydrate (Wittmann 1965), and mounted in 1:1 Hoyer's medium in distilled water according to the procedure of Hommersand and Fredericq (1988). Alternatively, sections were stained with 1% aniline blue (Papenfuss 1937) to highlight cytoplasmic contents. Stained sections were examined and photographed with a photomicroscope (Carl Zeiss Inc., Thornwood, NY, USA) using bright-field microscopy and T-Max 100 black and white film (Eastman Kodak Co., Rochester, NY, USA). Herbarium abbreviations follow Holmgren et al. (1990). Material used in this study is deposited at NCU.

The order of species descriptions in the Results begins with the generitype species, *Gracilaria bursa-pastoris*, and proceeds from the most familiar to the least familiar morphological forms. This is done to preserve continuity in the development of the terminology. The ordering of the groups covered in the Discussion and in Table 1 corresponds to our best estimate of the correct phylogenetic order.

#### RESULTS

1. *Gracilaria bursa-pastoris* (S. G. Gmelin) P. C. Silva (1952, p. 265)  
*Fucus bursa-pastoris* S. G. Gmelin (1768, p. 121)

*Lectotype*: Figure (plate 8, fig. 3) in Gmelin (1768).  
*Type locality*: Mediterranean Sea.

*Ceramiantemum ramosissimum humile, pellucidum, rubrum* Donati (1753, p. 26, pl. 1, fig. I; 1758, p. 27, fig. 8)

*Gracilaria compressa* (C. Agardh) Greville (1830, p. liv, 121) (Generitype species of *Gracilaria* Greville [1830]; see Steentoft et al. 1991)

*Sphaerococcus compressus* C. Agardh (1822, p. 308)

*Lectotype*: LD 28984, a tetrasporic plant collected by Antonio Cabrera and deposited in the Agardh herbarium; lectotype selected by C. J. Bird in 1979.

*Lectotype locality*: Cádiz (Gades), Spain; see Steentoft et al. (1991).

*Specimens examined*: Le Caro, Finistère, Brittany, France, 08.x.1991, leg. J. Cabioch; The Fleet, Dorset, England, UK, 19.ix.1993, leg. C. A. Maggs.

*Description*: Thallus 15–20 (–35) cm tall, attached by a small discoid holdfast; axes cartilaginous, terete, becoming compressed, often strongly so at points of branching (Fig. 1a), only slightly so in other portions; branches alternate or secund, to 4 mm diameter, gradually tapering toward the tips, sometimes with short proliferous branchlets on distal portions. Cystocarps dome-shaped (Fig. 1b), the gonimoblasts consisting of vacuolate cells in center toward the base, becoming elongated and highly branched toward the outside and bearing carposporangia in branched chains (Fig. 1, b and c), the carposporangia cut off by oblique division with the carpospores terminal, maturing basipetally, each with a darkly staining nucleus and distinct chromocenters (Fig. 1d); gonimoblast tubular cells numerous, variable in diameter, connecting to outer pericarp (Fig. 1, c and d), initially fusing with a single pericarp cell (Fig. 1f) that then may fuse progressively with neighboring pericarp cells extending the length of the tube to form a tube-shaped pericarp fusion cell (Fig. 1, c and d) that sometimes leaves behind unfused pit connections (Fig. 1e); carpogonial fusion cell with numerous enlarged nuclei, extending moderately by fusion with adjoining inner pericarp cells (Fig. 1g) and embedded longitudinally in the inner pericarp (Fig. 1h); cystocarp cavity formed schizogenously as the gonimoblasts grow, evidently by dissolution of pit connections between inner and outer pericarp filaments; inner pericarp composed of straight cell rows five to seven cells long in which each cell contains an enlarged nucleus (Fig. 1h). Male and tetrasporangial stages have been described and illustrated by Gargiulo et al. (1992). Hair-producing cells embedded among cortical cells, multinucleate, clavate to ovate, to 50 µm

TABLE 1. Morphological data pertaining to species groups in Gracilariaceae in estimated phylogenetic order.

	Abscissa group (Melanthalia)	Flabellata group (Curdiea)	Lemaneiformis group (Gracilarlopsis)	Chilensis group	Edulis group (Plocaria/Poly- cavernosa)	Urvillei group (Hydropuntia)	Crassissima group	Salicornia group (Corallopsis)	Gracilis group	Bursa-pastoris group (Gracilaria)
Organization of the sperm-antangia or male conceptacles	Unreported, thought to be superficial	In superficial nemathecia on secondary cortical filaments	Usually in a continuous layer from surface cortical cells	In shallow pits bordered by clavate cortical cells	Multicavitated by cavity extension	Multicavitated by cavity extension and conceptacle fusion	Multicavitated by cavity extension and conceptacle fusion	In deep pits lined by compressed cortical cells	In deep pits lined by compressed cortical cells	In shallow pits separated by little modified cortical cells
Formation of the sperm-antangia	Unknown	In tight clusters by concavo-convex septa, covered by a thick cuticle	In pairs, by oblique and transverse divisions of surface cortical cells	From spermatangial mother cells lining shallow to deep pits.	From spermatangial filaments originated from subcortical cells	From spermatangial filaments	From spermatangial filaments secondarily pit-con-nected to inner cortical cells	From spermatangial filaments from subcortical cells	From spermatangial filaments from subcortical cells	From spermatangial filaments, surface or subcortical cells
Type of fusion cell	Medium, limited secondary fusions	Medium, small fusion network	Small, with few secondary fusions	Small	Small, little or no secondary fusions	Medium, with some secondary fusion	Large, reticulate, secondary fusions	Medium, some secondary fusion	Large extensive secondary fusion	Medium, some secondary fusion
Modification of gametophytic cells in cystocarp floor	Thickened region of cells with enlarged nuclei	Cytologically unmodified	Cytologically modified multinucleate cortical cells	Laterally stretched multinucleate gametophytic cells	Floor concave, cytologically little modified	Floor concave cytologically somewhat modified?	Floor concave, cytologically somewhat modified	Cytologically modified, enlarged nuclei	Cytologically modified, multinucleate with enlarged nuclei	Cytologically little modified, excluding inner pericarp
Presence and modification of cells of inner pericarp	Inner pericarp cells lateral to fusion cell	Inner pericarp cells lateral to fusion cell	Inner pericarp cells lateral to fusion cell	Absent	Inner pericarp cells lateral to fusion cell	Inner pericarp lateral to fusion cell	Conspicuous inner pericarp lateral to the fusion cell	Inner pericarp lateral to fusion cell	Inner pericarp lateral to fusion cell	Inner pericarp lateral to the fusion cell
Gonimoblast connections to cystocarp floor	By secondary pit connections and cell fusions	By direct fusion of inner gonimoblast cells with inner pericarp cells	By conjunc-tory cells and secondary pit con-nections to inner pericarp cells	By short tubu-lar cells to cells with multiple secondary pit connections	By short tubular cells linked to a fusion network of stellate cells	By tubular cells linked to simple or branched tubular fusion cells	By tubular cells and dendritic fusion cells in inner pericarp	By tubular cells linked to branched fusion cells at base of pericarp cells.	By tubular cells linked to laterobasal tubular fusion cells.	Absent or highly reduced
Gonimoblast connections to outer pericarp	Absent	Absent	Absent	Absent	Absent	linked to tubular fusion cells	Generally absent, tubular fusion cells present in some	By tubular cells linked to tubular fusion cells	By tubular cells linked to tubular fusion cells	By tubular cells linked to tubular fusion cells
Initiation of cystocarp cavity	Around fusion cell at time of gonimoblast initiation	Around fusion cell and between inner and outer pericarp	Around fusion cell and modified cells lateral to fusion cell	Above developing gonimoblasts?	Around fusion cell and between inner and outer pericarp	Around fusion cell and between inner and outer pericarp	Schizogenous, above fusion cell and inner pericarp	Around the fusion cell and developing gonimoblasts	Above the fusion cell and inner pericarp	Above the fusion cell and inner pericarp
Method of cystocarp cavity formation	By dissolution of primary pit connections between pericarp cells	By dissolution of primary pit connections between inner and outer pericarp	By dissolution of primary pit connections between inner and outer pericarp	Not reported	Progressive, by separation of pericarp filaments above gonimoblasts	By dissolution of primary pit connections between inner and outer pericarp	By dissolution of primary pit connections between inner and outer pericarp	Progressive, by separation of pericarp filaments above the gonimoblasts	By dissolution of primary pit connections between inner and outer pericarp	By dissolution of primary pit connections between inner and outer pericarp
Ostiole formation	Bidirectional within pericarp	Unidirectional, distal to fusion cell	Unidirectional, distal to fusion cell	Not reported	Bidirectional, within pericarp	Bidirectional within pericarp	Bidirectional within pericarp	Unidirectional, distal to fusion cell	Unidirectional, distal to fusion cell	Unidirectional, distal to fusion cell

TABLE 1. (Continued)

	Abscissa group (Melanthalia)	Flabellata group (Curdiea)	Lemneiformis group (Gracilariaopsis)	Chilensis group	Edulis group (Plocaria/Poly- cavernosa)	Urvillei group (Hydroponitia)	Crassissima group	Salicornia group (Corallopsis)	Gracilis group	Bursa-pastoris group (Gracilaria)
Inner gonimoblast	Rectangular cells in radial rows cross- linked by secondary pit connections	Forms a fusion network with cells of the inner pericarp, no vacuolate cells	Reticulate network of isodiametric cells that become rectilinear with stretching	Network of large, isodiametric, vacuolate cells	Reticulate network of ovoid to fusiform vacuolate cells	Reticulate network of ovoid to fusiform vacuolate cells	Reticulate network of small laterally pit-connected cells	Reticulate network of ovoid vacuolate cells	Reticulate network of large ovoid vacuolate cells	Network of small elongate, laterally pit- connected cells
Outer gonimoblasts and carpo- sporangial chains	In radial rows with occasional branches	In vertical rows of unbranched or little branched chains	Forming a mantle of branched, short-chained filaments	A mantle of radially aligned branched chains	In short- branched chains at gonimoblast periphery	In short- branched chains at gonimoblast periphery	Short vertical chains with intercalary branching	Formed in clusters and maturing in files of branched chains	Formed in clusters and maturing in files of branched chains	In branched chains with carpospores cut off obliquely
Formation of the tetrasporangia	Nemathecial, by oblique division from surface cells	Nemathecial, by oblique division from surface cells	By oblique division from surface cells	Superficial in an unmodified cortex	Superficial in an unmodified cortex	Embedded in cortex surround- ed by files of cortical cells	Superficial in an unmodified cortex	Not reported	By oblique division from outer cortical cells	From terminal cortical cells

long, each usually with a remnant pit connection at the tip and swollen near the base (Fig. 1i); division in lower third of cell initiated by a furrow from one side (Fig. 1j) until a concavo-convex septum cuts off a basal cell (Fig. 1k) that undergoes lobing, flattening, and cytoplasmic change (Figs 1, l and m) while remaining pit connected to parent and neighboring cells (Fig. 1n) and eventually taking its place among other cortical cells.

2. *Gracilaria beckeri* (J. Agardh) Papenfuss (1952, p. 175)  
*Tyleiophora beckeri* J. Agardh (1890, p. 36) (as *beckeri*)  
*Tylothus beckeri* (J. Agardh) Kylin (1932, p. 60, figs. 17a, b, pl. 22, fig. 55)

*Lectotype:* Herb Agardh, LD #29837, lower left specimen "Hab ad Cap. b. Spei; specimina misit Holmes", selected and illustrated by Kylin (1932, pl. 22, fig. 55).

*Isotypes:* Other specimens on sheet LD #29837, LD #29828, LD #29835.

*Type locality:* "ad Cap. b. Spei," but probably mouth of the Kowie River, Port Alfred, Cape Province; see Silva et al. (1996).

*Specimens examined:* The Kowie, Port Alfred, Cape Province, South Africa, 30.vi.1983, leg. M. H. Hommersand; drift, Sharks Bay, The Kowie, South Africa, 04.xii.1983, leg. M. H. and F. C. Hommersand; Second Sister, Riet River, South Africa, 10.viii.1983, leg. M. H. Hommersand.

*Description:* Thallus bushy, erect to 25 cm tall, arising from a discoid holdfast and cylindrical to slightly compressed stipe, 0.8–1.8 cm long, 2 mm diameter; branches membranous to cartilaginous, strap shaped, to 6 mm wide, with finely and irregularly dentate margins throughout, wavy; commonly unequally dichotomous, proliferous at the distal portions, with rounded or, at times, truncate apices (Fig. 2a). Cystocarps borne on both sides of the flat surfaces, dome shaped, with slight basal constrictions (Fig. 2b) and central openings (Fig. 2d); gonimoblasts composed of slender tightly packed cells, bearing carposporangia in short branched chains (Fig. 2b); gonimoblast tubular cells multinucleate, connecting to pericarp cells that form linear tubes with lateral knobs that extend lengthwise through the pericarp by linear and lateral fusion of pericarp cells (Fig. 2c); carpogonial fusion cell multinucleate, expanding laterally as it incorporates neighboring cells (Fig. 2e); cortex (at least in cystocarpic plants) composed of two layers of densely pigmented cells, spherical, subtended by medullary cells (Fig. 2f). Spermatangial conceptacles scattered over thallus surface, embedded in the cortex and forming shallow pits with wide distal openings; spermatangia formed from filaments lining conceptacle floor and lower half of side walls, with the upper half flanked by clavate, arching uninucleate cells (Fig. 2g); adjacent concep-

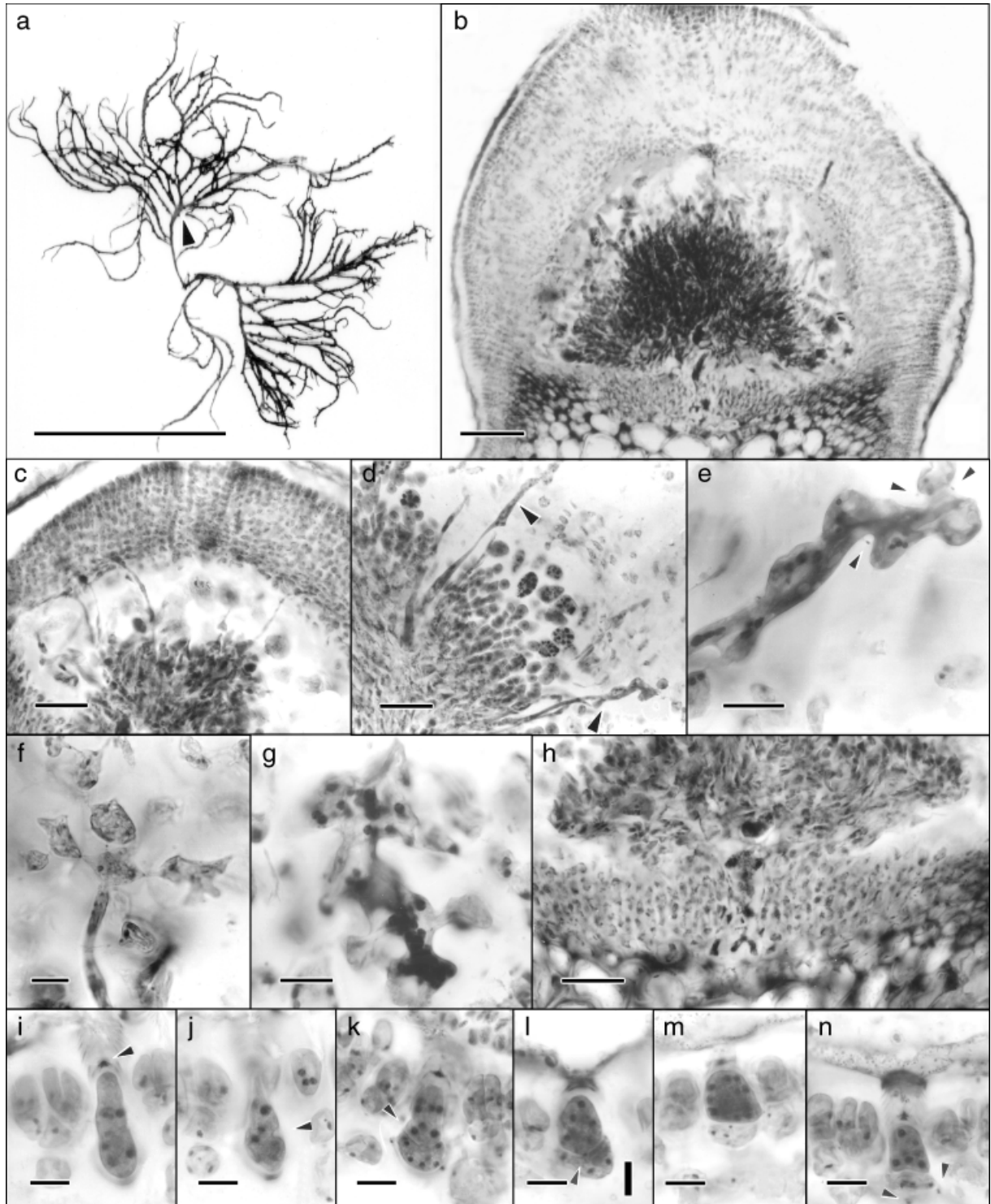


FIG. 1. *Gracilaria bursa-pastoris* (a, d–g, i–n = Finistère, France; b, c, h = Dorset, England). (a) Habit, cystocarpic plant. Scale, 5 cm. (b) Median section of mature cystocarp. Scale, 200  $\mu$ m. (c) Gonimoblasts with tubular cells connecting to pericarp. Scale, 100  $\mu$ m. (d) Gonimoblasts with tubular cells, tubular pericarp fusion cell (arrowhead), and carposporangial initials. Scale, 100  $\mu$ m. (e) Tubular pericarp fusion cell seen in d, showing remnant pit connections (arrowheads). Scale, 20  $\mu$ m. (f) Tubular cell fused to pericarp cell that is undergoing fusion with neighboring cells. Scale, 20  $\mu$ m. (g) Multinucleate gonimoblast fusion cell linking with neighboring cells. Scale, 20  $\mu$ m. (h) Degenerating fusion cell embedded in inner pericarp. Scale, 100  $\mu$ m. (i–n) Stages in the transformation of hair-producing cells. Description in text. Scale, 20  $\mu$ m.

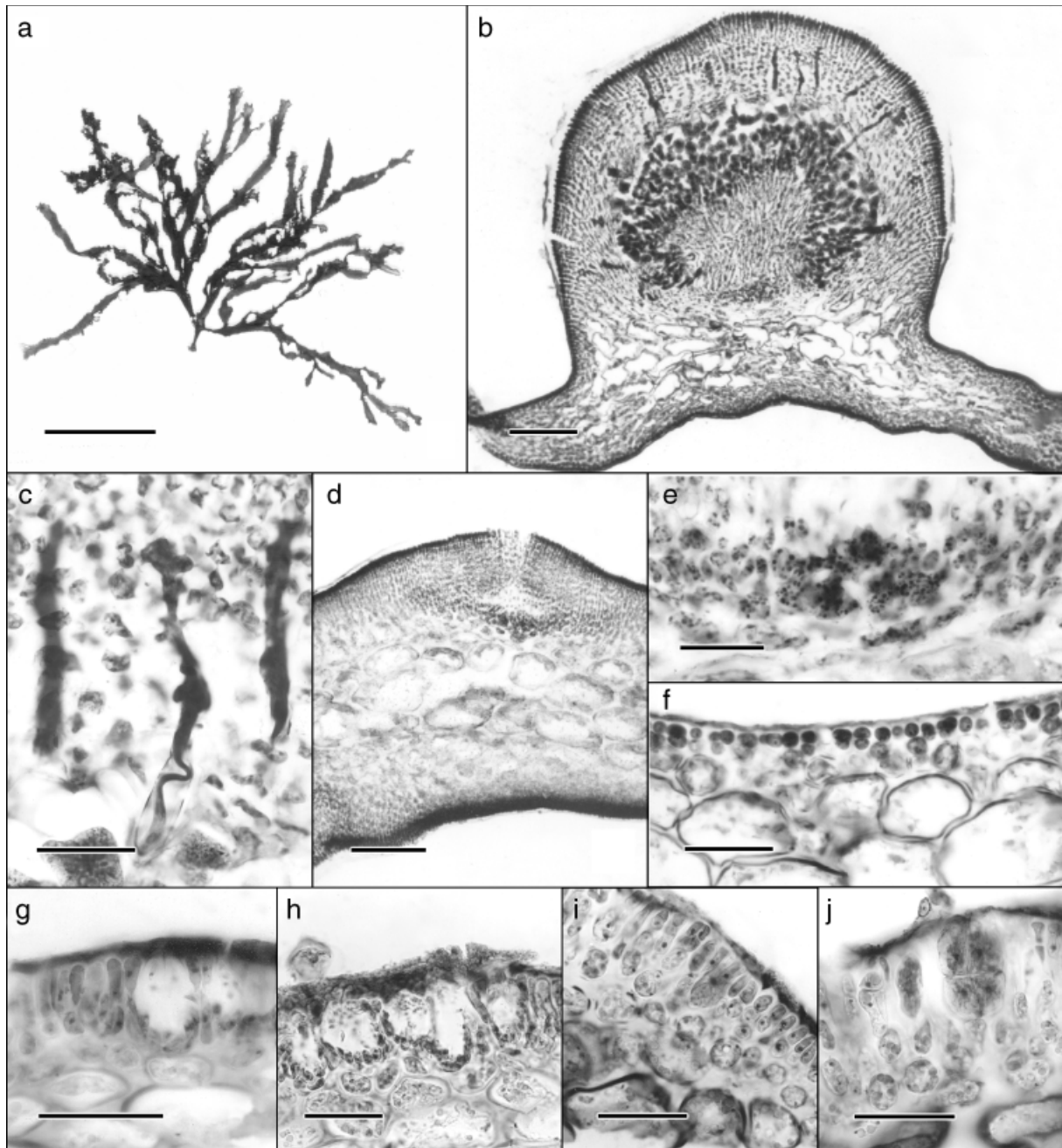


FIG. 2. *Gracilaria beckeri* (Port Alfred, South Africa). (a) Habit of cystocarpic plant. Scale, 5 cm. (b) Oblique section of cystocarp showing gonimoblasts, tubular cells, and tubular pericarp fusion cells. Scale, 200  $\mu$ m. (c) Close-up of tubular cells and tubular pericarp fusion cells. Scale, 50  $\mu$ m. (d) Cystocarp with developing cystocarp cavity and ostiole. Scale, 200  $\mu$ m. (e) Multinucleate gonimoblast fusion cell. Scale, 50  $\mu$ m. (f) Transverse section of female plant showing medulla and cortical layer composed of spherical cells. Scale, 50  $\mu$ m. (g) Spermatangial conceptacles in shallow pits flanked by elongate cortical cells. Scale, 50  $\mu$ m. (h) Confluent spermatangial conceptacles. Scale, 50  $\mu$ m. (i) Transition zone between cortical layer (right) and tetrasporangial nemathecium (left). Scale, 50  $\mu$ m. (j) Tetrasporangial nemathecium with cruciately divided tetrasporangium. Scale, 50  $\mu$ m.

tacles developing asynchronously (as evidenced by variable conceptacle depths) and often coalescing (Fig. 2h). Tetrasporangia formed in distinct darkly pigmented nemathecium on both thallus surfaces 0.5 mm inside the margins, nemathecium composed of chains of elongated cortical cells formed by transverse and occasional oblique divisions of surface cortical cells

(Fig. 2i); tetrasporangia cruciately divided, surrounded by chains of elongated cortical cells (Fig. 2j).

3. *Gracilaria salicornia* (C. Agardh) Dawson (1954, p. 4, fig. 3)
- Sphaerococcus salicornia* C. Agardh (1820, pl. VIII, figs. 1–4)

*Corallopsis salicornia* (C. Agardh) Greville (1830, p. liii)  
(for suggested taxonomic synonyms, see Xia [1986] and Silva et al. [1996])

*Holotype*: A collection by Adelbert von Chamisso during the Romanzov exploring expedition (1815–1818) in Herb Agardh LD #28699.

*Type locality*: recorded by C. Agardh (1820) as Unalaska in the Aleutian Islands, but probably Manila Bay, Philippines *vide* Dawson (1954, p. 4).

*Specimens examined*: Morib, Selangor, Malaysia, 09.v.1992, leg. Pozi Milow; Starfish Island, Honda Bay, Palawan, Philippines, 09.iv.1989, leg. M. H. Hommersand; Maribago, Mactan Island, Cebu, Philippines, 06.iii.1992, leg. Danilo B. Largo.

*Description*: Thallus 12–15 cm tall, cartilaginous, composed of clavate segments joined end to end (Fig. 3a); segments terete, to 20 mm long, tapered at the proximal ends, gradually becoming inflated toward the distal ends to 3 mm diameter; branches opposite to dichotomous, issuing from pits on swollen apices. Cystocarps dome shaped, with ostiole at top (Fig. 3b); gonimoblasts composed of loosely arranged ovoid vacuolate cells bearing clusters of carposporangia at periphery in short branched chains (Fig. 3c); gonimoblast tubular cells extending to top, sides, and base of outer pericarp (Figs. 3, c and d, and 4b), multinucleate, inflated toward base (Fig. 3e), sometimes with more than one tubular cell attaching to a pericarp cell (Fig. 3g); pericarp fusion cells tubular (above) or branched (below) (Fig. 3d); pericarp cells arranged regularly in young cystocarps (Fig. 4b), the inner layers darkly staining and stretched laterally at maturity (Fig. 3, b and f); carpogonial fusion cell multinucleate, cubic to ovoid in young carposporophytes (Fig. 4a), compressed in older cystocarps, embedded within inner pericarp (Fig. 3h). Spermatangial conceptacles confined to unevenly distributed soral patches, forming deep pits embedded in the cortex, each with a narrow opening to the outside (Fig. 4, c and d) and with slender compressed cortical cells attached to the outer conceptacle wall (Fig. 4e). Tetrasporangial stages were not seen. Hair-producing cells globose, multinucleate, more darkly staining than surrounding cells, 20 µm across (Fig. 4f), becoming shriveled and convoluted soon after the hair is shed, with a remnant pit connection at the tip (Fig. 4g), eventually becoming vacuolate, periclinally compressed and lobed while maintaining its pit connection with the cell below (Fig. 4, h and i).

4. *Gracilaria edulis* (S. G. Gmelin) Silva (1952, p. 293)  
*Fucus edulis* S. G. Gmelin (1768, p. 113)

*Lectotype*: Figures (pl. 74, Fig. 3, pl. 76, Figs. A–C) in Rumphius (1750), reproduced in Abbott (1994, figs 1–4); the original collection by George Everhard Rumpf (commonly Latinized as Rumphius) and published as “Alga coralloides.” This specimen,

together with others in the Rumphius collection, was presumably lost during the fire that burned down his house in Amboina (Ambon) Island, East Indies (in present-day Indonesia) on 11 January 1687.

*Type locality*: India orientalis, referring to various sites in the East Indies.

*Plocaria candida* Nees (1820, p. 42, pl. 7).

*Lectotype*: Figures (pl. 7) in Nees (1820). The original collection is presumed to have been housed in Berlin where it was destroyed during World War II.

*Type locality*: Bay of Bengal.

*Polycaavernosa fastigiata* Chang et Xia (1963, p. 120, pl. 1, figs. 1–12, pl. 2, figs. 1–6)

*Hydropuntia fastigiata* (Chang et Xia) Wynne (1989, p. 477)

*Holotype*: AST 60-7240 (female).

*Type locality*: Yingghai, Ledung District, Hainan I., Kwangtung Prov., China.

*Gracilaria lichenoides* (Lamouroux) Greville (1830, p. liv, *nom. illeg.*)  
(for additional synonyms, see Silva et al. [1996])

*Specimens examined*: Morib, Selangor, Malaysia, 09.v.1992, leg. Pozi Milow; Bagacay, Gubat, Sorsogon, Philippines, 21.iv.1994, leg. A. Hurtado-Ponce; Yingghai, Ledung, Hainan Island, China, 29.iv.1980, leg. Xia Bangmei ex herb. S. Fredericq.

*Description*: Thalli forming clumps, to 13 cm tall, attached by rhizomatous base, terete throughout, to 2 mm diameter, branching alternately, frequently so toward apices, without constrictions at bases of branches; highest order branches usually bifid, tapered gradually to acute tips (Fig. 5a). Cystocarps globose, dome shaped (Fig. 5b), to 1.5 mm diameter, slightly constricted at the bases of mature cystocarps (Fig. 5e); gonimoblast cells ovoid to fusiform, forming a spherical central mass (Fig. 5f), the carposporangia borne peripherally in short chains that branch basally by oblique divisions (Fig. 5c), with the carposporangia terminal, maturing basipetally (Fig. 5d); tubular cells issuing only from gonimoblast base and fusing with cells of the inner pericarp (Fig. 5g), these, in turn, uniting to form a network of darkly staining stellate fusion cells (Figs. 5g and 6a); innermost cells of the outer pericarp not stretching during cystocarp enlargement but separating into dangling fascicles of radial files (Fig. 6b), especially near the ostiole (Fig. 6c). Spermatangial conceptacles protruding slightly from the surface at maturity (Fig. 6d); young conceptacles embedded in the cortex, multicavitated, the cavities separated by thin layers of wall material (Fig. 6, e and f), with a single opening formed above the level of the surface cortical cells, probably by the rupture of an outer cuticle (Fig. 6e); cavities enlarging



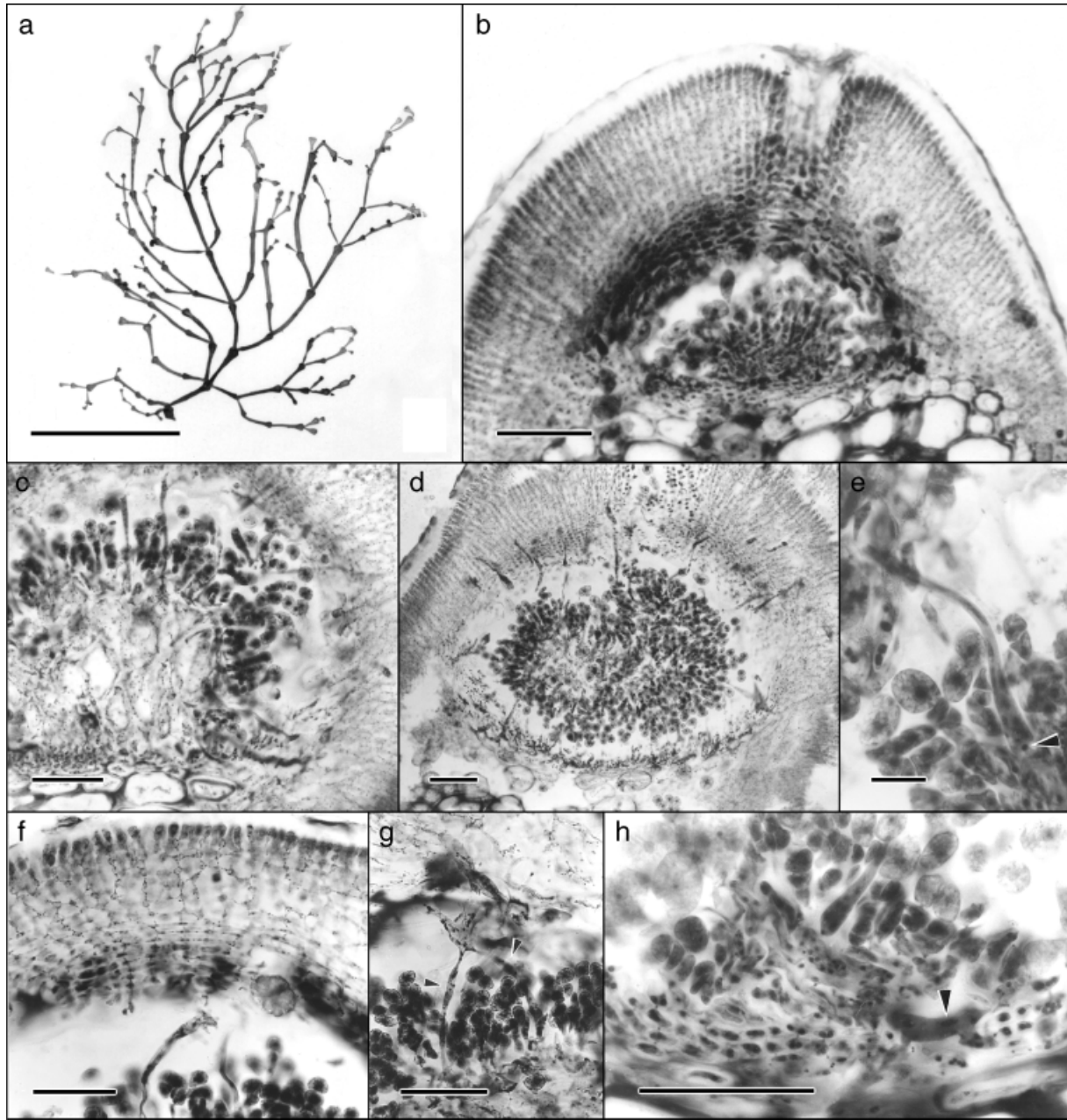


FIG. 3. *Gracilaria salicornia* (a = Palawan, Philippines; b–h = Selangor, Malaysia). (a) Habit of a male plant. Scale, 5 cm. (b) Median section of a mature cystocarp. Scale, 100  $\mu$ m. (c) Gonimoblasts bearing carposporangial chains and tubular cells connecting to outer and lower edge of pericarp. Scale, 100  $\mu$ m. (d) Oblique section of cystocarp showing extensive tubular cells and tubular fusion cells in outer pericarp and tubular cells and branched fusion cells at lower edge of pericarp. Scale, 100  $\mu$ m. (e) Carposporangial chains and inflated base of tubular cell attached to gonimoblast by a pit connection (arrowhead). Scale, 20  $\mu$ m. (f) Tubular cell connected to inner pericarp cell. (Note laterally stretched internal pericarp layers.) Scale, 100  $\mu$ m. (g) Gonimoblasts bearing carposporangial chains and two tubular cells (arrowheads) fused to the same pericarp cell. Scale, 20  $\mu$ m. (h) Degenerating fusion cell (arrowhead) embedded in modified inner pericarp. Scale, 100  $\mu$ m.

in all directions displacing neighboring cortical cells and compressing them while maintaining their pit connections (Fig. 6e), sometimes surrounding a cortical cell during enlargement (Fig. 6f); breakdown of cross walls between globular portions of multicavitated conceptacle sometimes resulting in a single large-lobed conceptacle (Fig. 6h); spermatangia cut off inwardly into conceptacle cavity from spermatangial parent cells (Fig. 6g).

Tetrasporangia subspherical, cruciately divided, slightly protruding with flattened or elongated cells present adjacent to the tetrasporangium (Fig. 6i).

5. *Gracilaria urvillei* (Montagne) Abbott in Abbott et al. (1991, p. 23)

*Hydropuntia urvillei* Montagne (1842, p. 7; 1845, pp. 166–168, pl. 1, fig. 1 [pl. 1 first published in 1843])



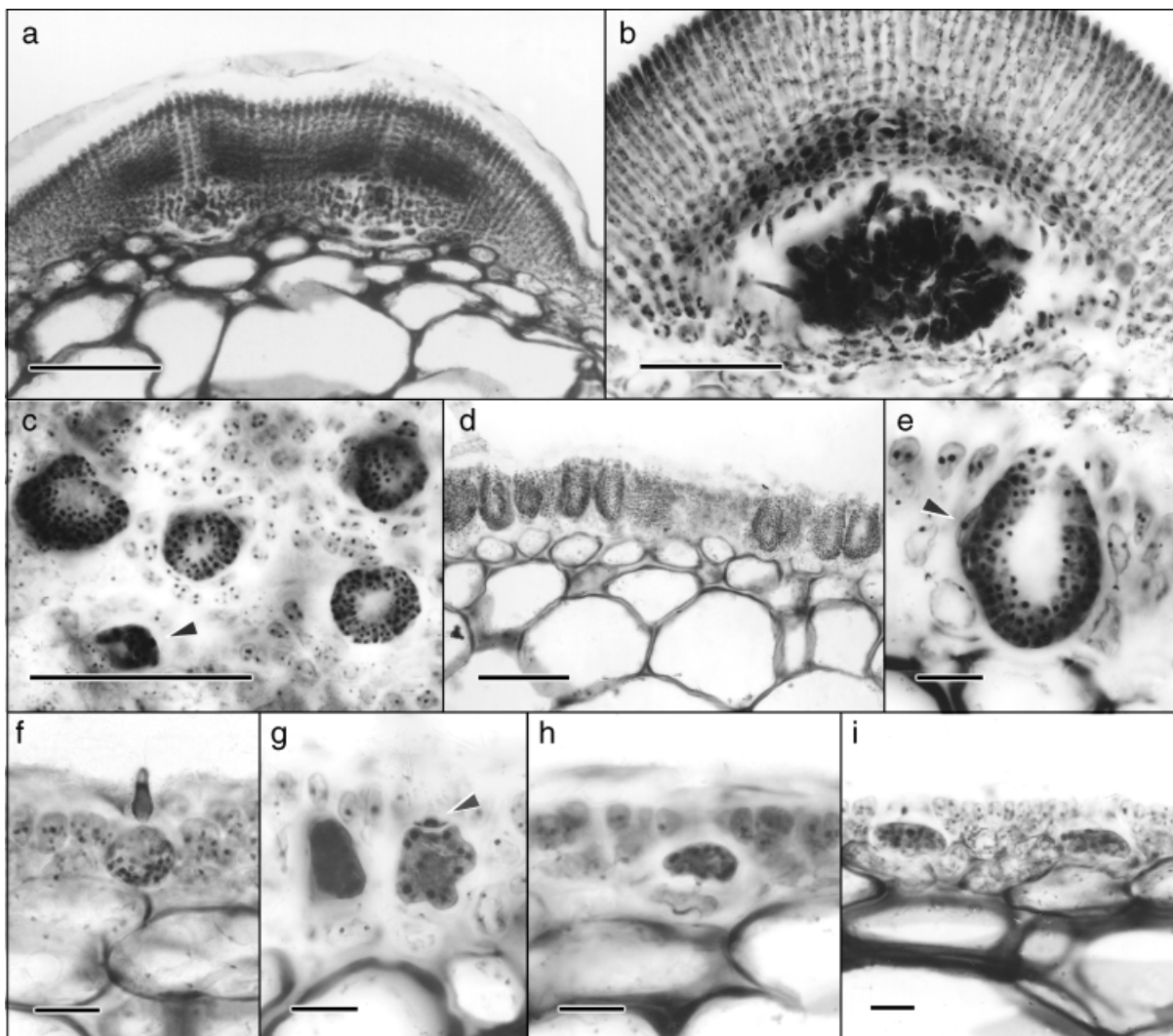


FIG. 4. *Gracilaria salicornia* (a, b, f, h = Selangor, Malaysia; c–e, g, i = Palawan, Philippines). (a) Two young cystocarps with fusion cells showing initiation of cystocarp cavities and ostioles. Scale, 100  $\mu$ m. (b) Near median section of young cystocarp. Scale, 100  $\mu$ m. (c) Surface view of spermatangial conceptacles. Arrowhead points to remnant hair-producing cell. Scale, 100  $\mu$ m. (d) Longitudinal section of spermatangial conceptacles. Scale, 100  $\mu$ m. (e) Transverse section of spermatangial conceptacle and compressed cortical cell (arrowhead) pit connected to its outer wall. Scale, 20  $\mu$ m. (f–i) Stages in the transformation of hair-producing cells. Description in text. Scale, 20  $\mu$ m.

*Corallopsis urvillei* (Montagne) J. Agardh (1852, p. 583)  
*Polycavernosa urvillei* (Montagne) Xia et Abbott (1987, p. 414, figs. 7, 8)

*Holotype*: A June 1840 collection by Dumont d'Urville during the voyage to the South Pole and Oceania in the corvettes *Astrolabe* and *Zélée* (1837–1840) and preserved at PC #MA3686-MA3689, including two mica slides, fragments, and two slides by I. A. Abbott.

*Type locality*: Ins. Toud in Freto Torres, present-day Warrior Reef in the Torres Strait, between northeastern Australia and southern Papua New Guinea where the two corvettes ran aground from 2–7 June 1840 (Rosenman 1987).

*Specimens examined*: Torres Strait, Challenger Expedition, leg. H. Moseley (BM); Cape York, N. Australia, Challenger Expedition, leg. H. Moseley (BM); BISH 568223, Pulo Karindingan, Semporna, Sabah, Malaysia, 25.vii.1979, leg. V. B. Alvarez (MD 28847); BISH 561954, Eilogo village, Sabu Island, Lesser Sunda Islands, Indonesia, XI 1987, leg. Steven Why (MSD 33095); NSW 293656, Brampton Island, off Mackay, Queensland, Australia, 18.vi.1948, leg. V. May 2731c; BRI 468700, Mud Cod Bay, Groote Eylandt, Northern Territory, Australia, 18.xi.1975, leg. J. Waddy 495; L 939.69.939, Straat Selee, Nieuw Guinea, 18.vii.1899, Siboga-Expeditie, leg. A. Weber-van Bosse.

*Description*: Thalli to 25 cm tall, cartilaginous, with percurrent axes (Fig. 7a), terete, at times slightly

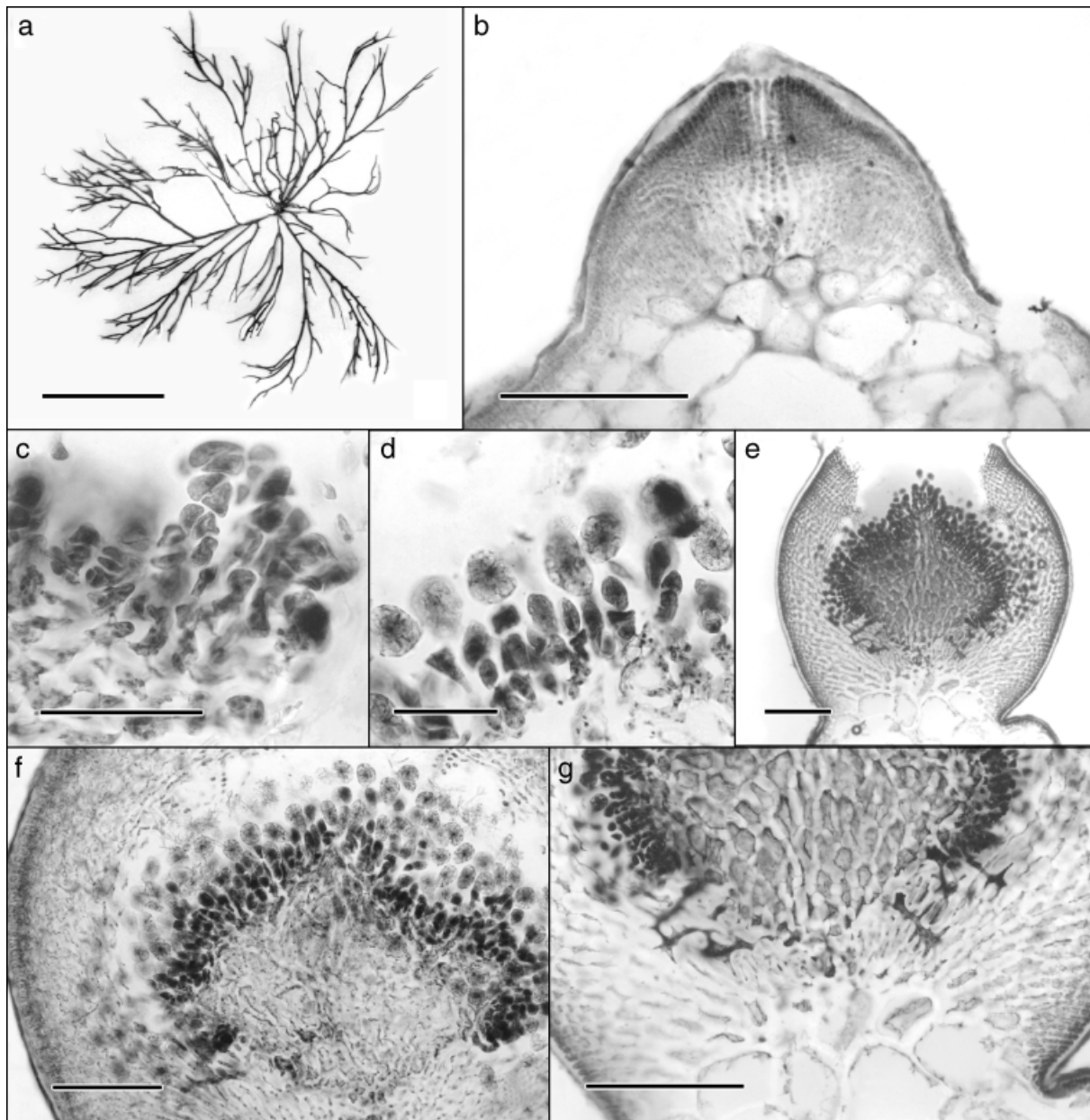


FIG. 5. *Gracilaria edulis* (a = Sorsogon, Philippines; b–g = Selanger, Malaysia). (a) Habit of cystocarpic plant. Scale, 5 cm. (b) Young cystocarp with dome-shaped pericarp showing the formation of the cystocarp cavity and ostiole. Scale, 200  $\mu$ m. (c) Gonimoblasts producing carposporangial chains undergoing oblique divisions. Scale, 50  $\mu$ m. (d) Carposporangial chains with terminal carposporangia. Scale, 50  $\mu$ m. (e) Median section of mature cystocarp showing basal constriction. Scale, 200  $\mu$ m. (f) Cystocarp showing the absence of tubular cells connecting gonimoblasts with outer pericarp. Scale, 200  $\mu$ m. (g) Gonimoblast cells issuing tubular cells that link to a basal fusion network. Scale, 200  $\mu$ m.

compressed, approximately 5–7 mm diameter, constricted at the nodes, each segment appearing pedicellate, tapered toward the base, becoming inflated distally (Fig. 7a), surfaces beset with irregularly disposed prickly outgrowths with acuminate tips; branches issuing from any part of thallus, but generally near the tips, strongly constricted at the bases. Cystocarps superficial, each with a basal constriction and an apical beak (Fig. 7b); gonimoblasts filling the cystocarp cavity (Fig. 7c), often coming into close contact with the outer pericarp

(Fig. 7d) composed of tightly packed fusiform cells bearing short carposporangial chains at periphery (Fig. 7h); gonimoblast tubular cells short, fusing with cells in the inner layer of the outer pericarp (Fig. 7g) that, in turn, fuse to form tubular pericarp fusion cells in oblique (Fig. 7e) or straight series (Fig. 7f); outer pericarp thick, composed of cell layers that may be divisible into light- and dark-staining bands (Fig. 7i) and laterally stretched inner layers. Spermatangial conceptacles scattered, embedded in the cortex and outer medulla (Fig. 8a); young conceptacles oval, in

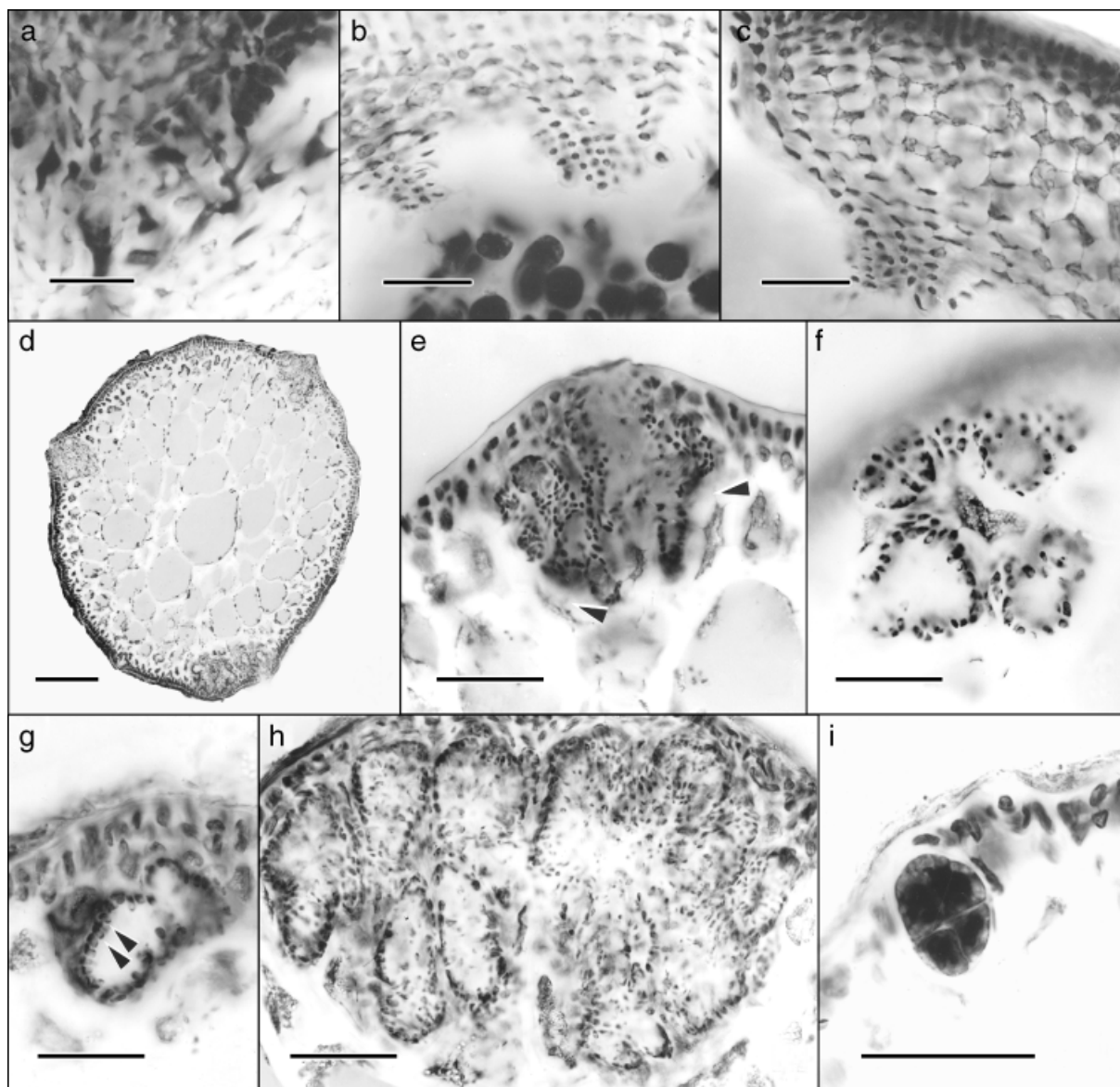


FIG. 6. *Gracilaria edulis* (a–c = Selanger, Malaysia; d, f–i = Sorsogon, Philippines; e = Hainan Island, China). (a) Close-up of tubular cells linking with fusion network in floor of cystocarp. Scale, 50  $\mu$ m. (b) Files of cells in the outer pericarp separating into fascicles. Scale, 50  $\mu$ m. (c) Pericarp files in fascicle near ostiole. Scale, 50  $\mu$ m. (d) Transverse section showing the raised appearance of spermatangial conceptacles. Scale, 200  $\mu$ m. (e) Median section of spermatangial conceptacle with opening under cuticle, showing compressed cortical cells (arrowheads) pit connected to conceptacle wall. Scale, 50  $\mu$ m. (f) cortical cell surrounded by lobes of the spermatangial cavity. Scale, 50  $\mu$ m. (g) Oblique section of spermatangial conceptacle showing spermatangia (arrowheads) produced from spermatangial parent cells. Scale, 50  $\mu$ m. (h) Oblique section of large spermatangial conceptacle with confluent cavities. Scale, 50  $\mu$ m. (i) Crucially divided tetrasporangium in little-modified cortex. Scale, 50  $\mu$ m.

deep pits surrounded by stretched subcortical cells (Fig. 8b), becoming lobed as they extend laterally (Fig. 8c) and longitudinally (Fig. 8d); with slender cortical cells lining the periphery of the lobes or sometimes lodged between the enfolding lobes (Fig. 8d); a single median pit connection typically linking between each subcortical cell and the conceptacle; external openings formed in young conceptacles (Fig. 8b), persisting in mature conceptacles (Fig. 8d). Tetrasporangia ellipsoid, twice as long as broad,

crucially divided, embedded in the cortex and surrounded by files of elongate cortical cells (Fig. 8, e and f). Hair-producing cells formed in circular patches (Fig. 8g), fusiform, clavate, to 40  $\mu$ m long, 15  $\mu$ m broad, with remnant pit connection at the tips (Fig. 8, g and h) and a basal cell cut off toward the inside (Fig. 8i).

6. *Gracilaria eucheumatoides* Harvey (1860, p. 331) (as *eucheumoides*; corrected in Silva et al. [1996])

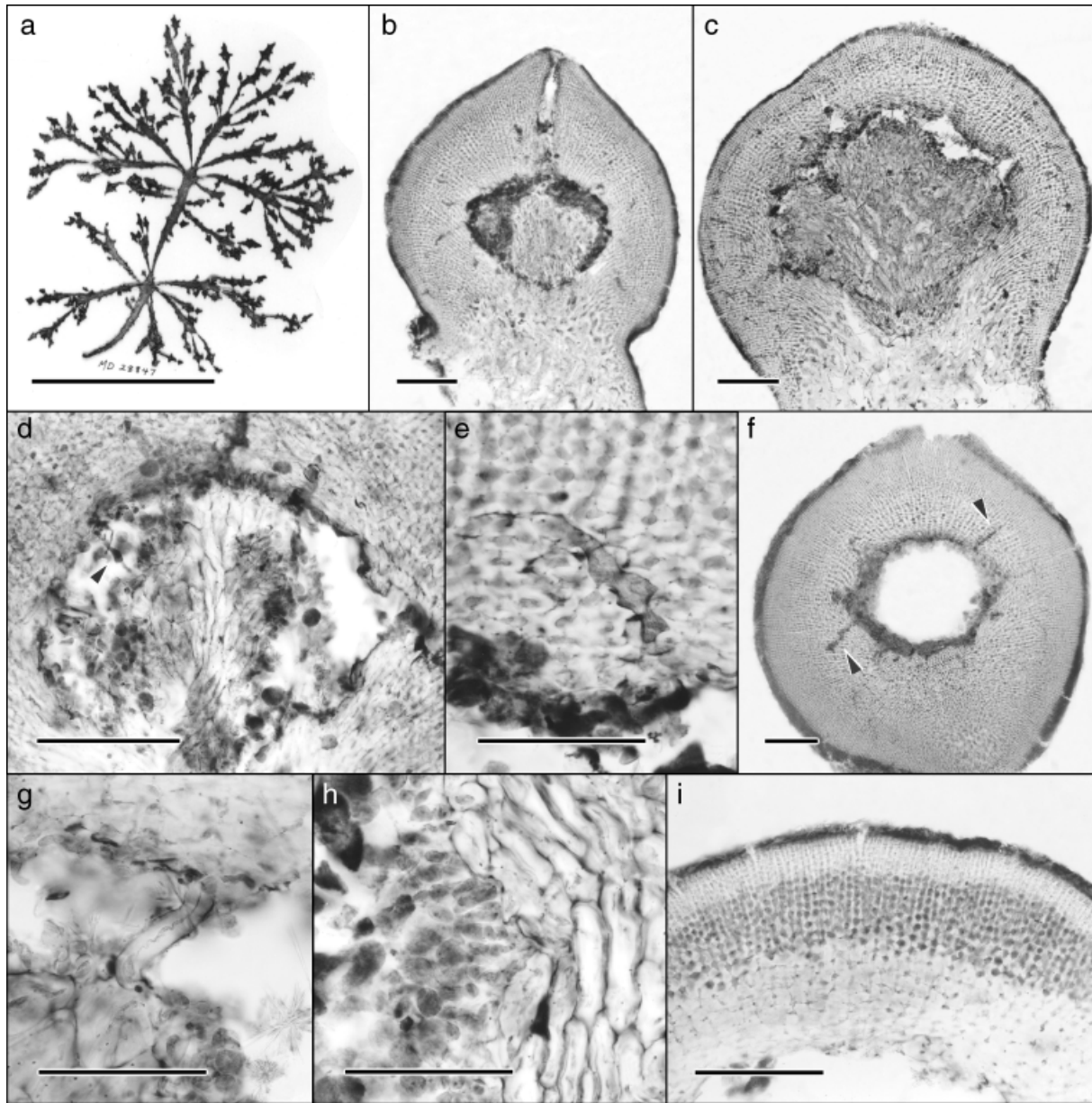


FIG. 7. *Gracilaria urovillei* (a = Sabah, Malaysia; b–d, g, h = Torres Straits, northern Australia; f, i = Cape York, Queensland, Australia). (a) Habit of a robust plant. Scale, 5 cm. (b) Median section of cystocarp with ostiole and gonimoblasts producing basal and peripheral fusion tubes. Scale, 200  $\mu$ m. (c) Oblique section of cystocarp with mature gonimoblasts. Scale, 200  $\mu$ m. (d) Mature gonimoblasts with tubular cells connecting to outer pericarp. Scale, 200  $\mu$ m. (e) Tubular pericarp fusion cell extending diagonally in outer pericarp. Scale, 100  $\mu$ m. (f) Oblique section showing tubular pericarp fusion cells in outer pericarp (arrowhead, upper right) and laterobasal pericarp (arrowhead, lower left). Scale, 200  $\mu$ m. (g) Two gonimoblast tubular cells fused with inner cells of the outer pericarp. Scale, 100  $\mu$ m. (h) Gonimoblasts with carposporangial chains. Scale, 100  $\mu$ m. (i) Bands of light- and dark-staining cells in the outer pericarp. Scale, 100  $\mu$ m.

*Lectotype*: a specimen at TCD collected by Charles Wright from the Ryukyu Islands, illustrated by Masuda et al. (1995, p. 195, fig. 14).

*Lectotype locality*: Ryukyu Islands, Japan, *vide* Masuda et al. (1995, p. 196).

*Specimens examined*: Tidepools near Nanliao fishport, Tao (Green Island), Taitung County, Taiwan, 16.xii.1992, leg. Jishan Chen and L. M. Liao.

*Description*: Thalli forming low, prostrate clumps, compressed, 4–5 mm thick, 7–10 mm broad, frequently overlapping, branching irregularly or dichotomously at the tips, the branches sometimes strongly constricted at the bases, attaching to one another by numerous haptera; margins blunt, beset with short spines or coarse, unevenly distributed teeth (Fig. 9a). Cystocarps borne along the margins and on the flattened surfaces, basally constricted, dome shaped,

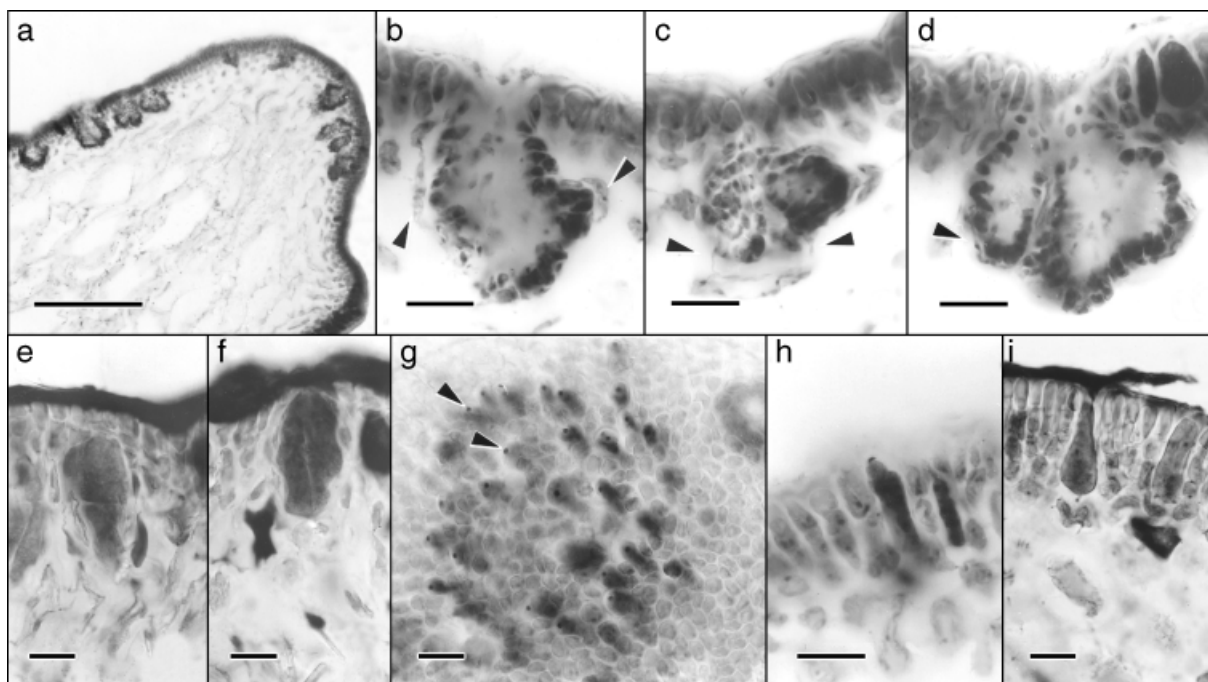


FIG. 8. *Gracilaria urvillei* (a–d, g, h = Brampton Island, Queensland, Australia; e, f = Sabu Island, Indonesia; i = Cape York, Queensland, Australia). (a) Transverse section showing spermatangial conceptacles. Scale, 200  $\mu$ m. (b–d) Stages of outpocketing of spermatangial conceptacles and elongated cortical cells pit connected to their outer walls (arrowheads). Scale, 20  $\mu$ m. (e and f) Developing and mature cruciately divided tetrasporangia surrounded by files of cortical cells. Scale, 20  $\mu$ m. (g) Surface view of a group of hair-producing cells showing remnant pit connections (arrowheads). Scale, 20  $\mu$ m. (h) Undivided hair-producing cell. Scale, 20  $\mu$ m. (i) Hair-producing cell and subtending basal cell embedded in files of cortical cells. Scale, 20  $\mu$ m.

with prominent beaks; gonimoblasts composed of ovoid inner cells (Fig. 9b) and bearing carposporangia in short branched chains; gonimoblast tubular cells multinucleate, connecting with cells of the outer pericarp and forming tubular extensions by progressive cell fusion (Fig. 9, c and d) or connecting with cells of the inner pericarp and forming club-shaped branched fusion cells (Fig. 9e); pericarp well developed in young cystocarps before gonimoblast initiation (Fig. 9f), initially three layered, consisting of an inner layer of multinucleate cells with enlarged nuclei, a middle layer of cells with darkly staining cytoplasm, and an outer layer of lightly staining cells (Fig. 9g); the inner layer ultimately incorporated into the expanding carpogonial fusion cell (Fig. 9f); cystocarp cavity initiated by the stretching and breakdown of cells between the middle and inner layers (Fig. 9h); fusion cell persistent in mature cystocarps, compressed (Fig. 9b). Male and tetrasporangial stages were not seen.

7. *Gracilaria aculeata* (Hering) Papenfuss (1967, p. 100)

*Sphaerococcus aculeatus* Hering (1841, pp. 91–92 *nom. illeg.*)

*Gelidium aculeatum* Hering in Krauss (1846, p. 210)

*Gigartina aculeata* (Hering) Kützting (1868, p. 3, pl. 6, figs. a, b)

*Corallopsis aculeata* (Hering) Holmes (1894, p. 336, pl. 18, figs. 16–20)  
(for additional synonyms see Silva et al. [1996])

*Holotype*: A collection by Ferdinand Krauss, in Hamburg (HBG). The illustration by Kützting (1868, pl. 6, fig. a) is evidently from a fragment of the *Holotype*.

*Type locality*: Natalbai (Port Natal), now Durban, South Africa.

*Specimens examined*: Reef at Glenmore Beach, Natal, South Africa, 19.xii.1977, leg. M. H. Hommersand; Second Sister, Riet River, Cape Province, South Africa, 10.viii.1983, leg. M. H. Hommersand; drift, Sharks Cove, The Kowie, Port Alfred, Cape Province, South Africa, 15.xii.1977, leg. M. H. Hommersand.

*Description*: Thalli bushy, cartilaginous, to 30 cm tall, attached to substrate by a discoid holdfast (Fig. 10a) and terete to slightly compressed stipe, to 8 mm long; main axes subdichotomously branched, slightly constricted, the ultimate branches with constricted bases, becoming terete, to 4 mm diameter, beset with mostly whorled spines to 1 mm high at more or less regular 3- to 4-mm intervals. Cystocarps scattered, dome shaped, with low beak (Fig. 10b); gonimoblasts composed of slender, loosely organized elongated cells bearing carposporangia in short branched chains (Fig. 10d); gonimoblast tubular cells connecting to cells of the inner layer of the outer pericarp



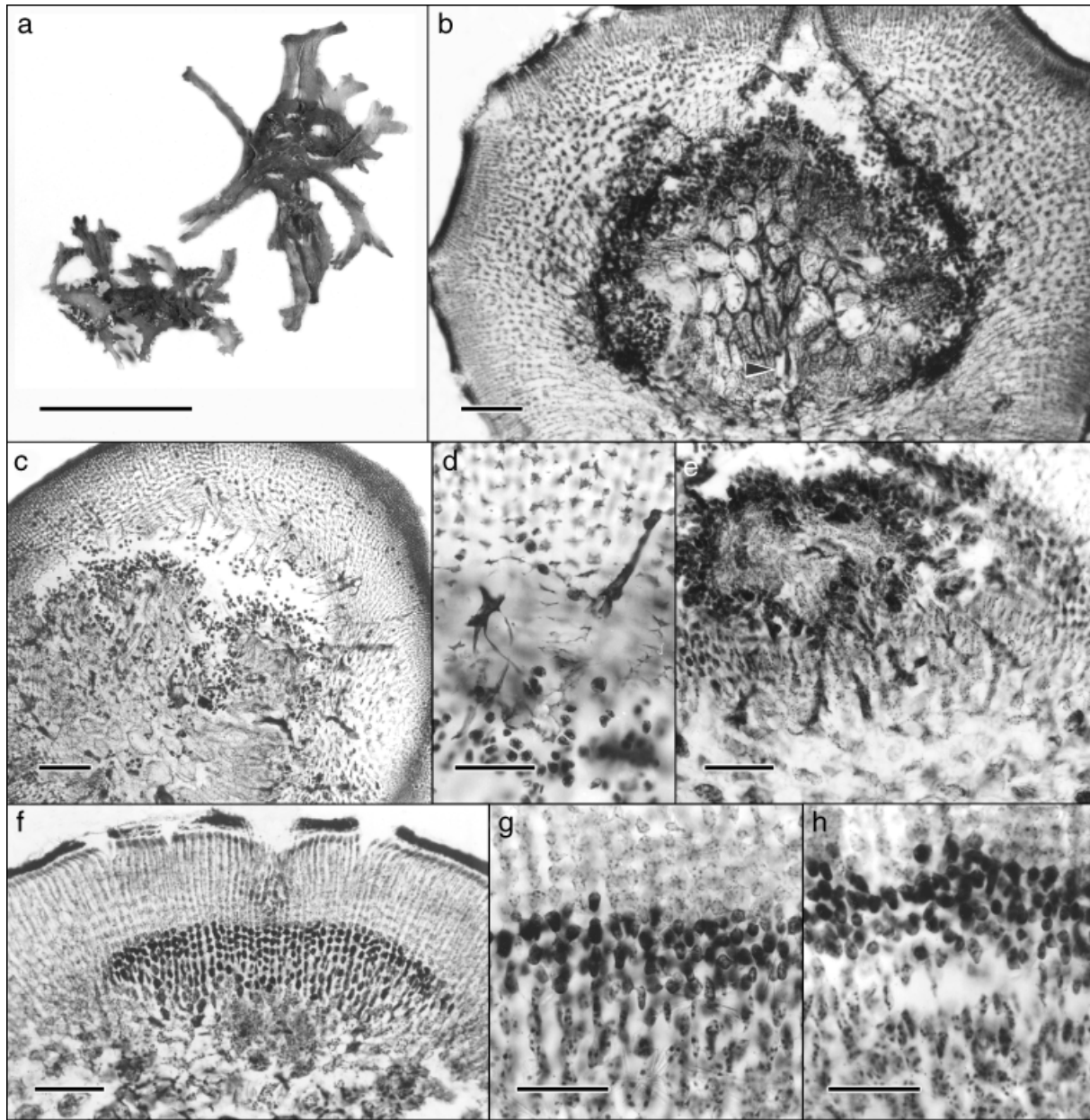


FIG. 9. *Gracilaria eucheumatoides* (Green Island, Taiwan). (a) Habits of two plants. Scale, 5 cm. (b) Median section of mature cystocarp showing gonimoblasts and compressed fusion cell (arrowhead). Scale, 200  $\mu\text{m}$ . (c) Oblique section showing tubular cells linking the gonimoblasts with the pericarp and tubular fusion cells in pericarp. Scale, 200  $\mu\text{m}$ . (d) Close-up showing tubular cells emanating from the gonimoblasts and linking to fusion cells in the outer pericarp. Scale, 100  $\mu\text{m}$ . (e) Oblique section of cystocarp showing tubular cells fusing with cells at base of pericarp connecting to branched tubular fusion cells. Scale, 100  $\mu\text{m}$ . (f) Young cystocarp with carpegonial fusion cell and well-developed pericarp with dark inner and light outer bands. Scale, 100  $\mu\text{m}$ . (g) Three-layered stage of pericarp development. Scale, 50  $\mu\text{m}$ . (h) Initiation of cystocarp cavity by separation between the middle and inner pericarp layers. Scale, 50  $\mu\text{m}$ .

(Fig. 10c), apparently not penetrating into the pericarp layers and without the formation of pericarp fusion cells (Fig. 10b), tubular cells also issuing from base of gonimoblasts and fusing with inner pericarp cells to form a branched filamentous fusion network (Fig. 10e); carpegonial fusion cell multinucleate, fusing with neighboring cells (Fig. 10g); young cystocarp with well-developed pericarp and broad base (Fig. 10f); formation of cystocarp cavity by

separation of inner and outer pericarp layers (Fig. 10f), with the ostiole forming simultaneously to the outside and inside (Fig. 10, b and f) initiated by dissolution of mid-regional pericarp cells (Fig. 10h). Male and tetrasporangial stages were not seen.

8. *Gracilaria chilensis* Bird, McLachlan et Oliveira (1986, pp. 2928–2929, Figs. 2–13)  
*Gracilaria sordida* Nelson (1987, pp. 90–91, figs. 6–9)

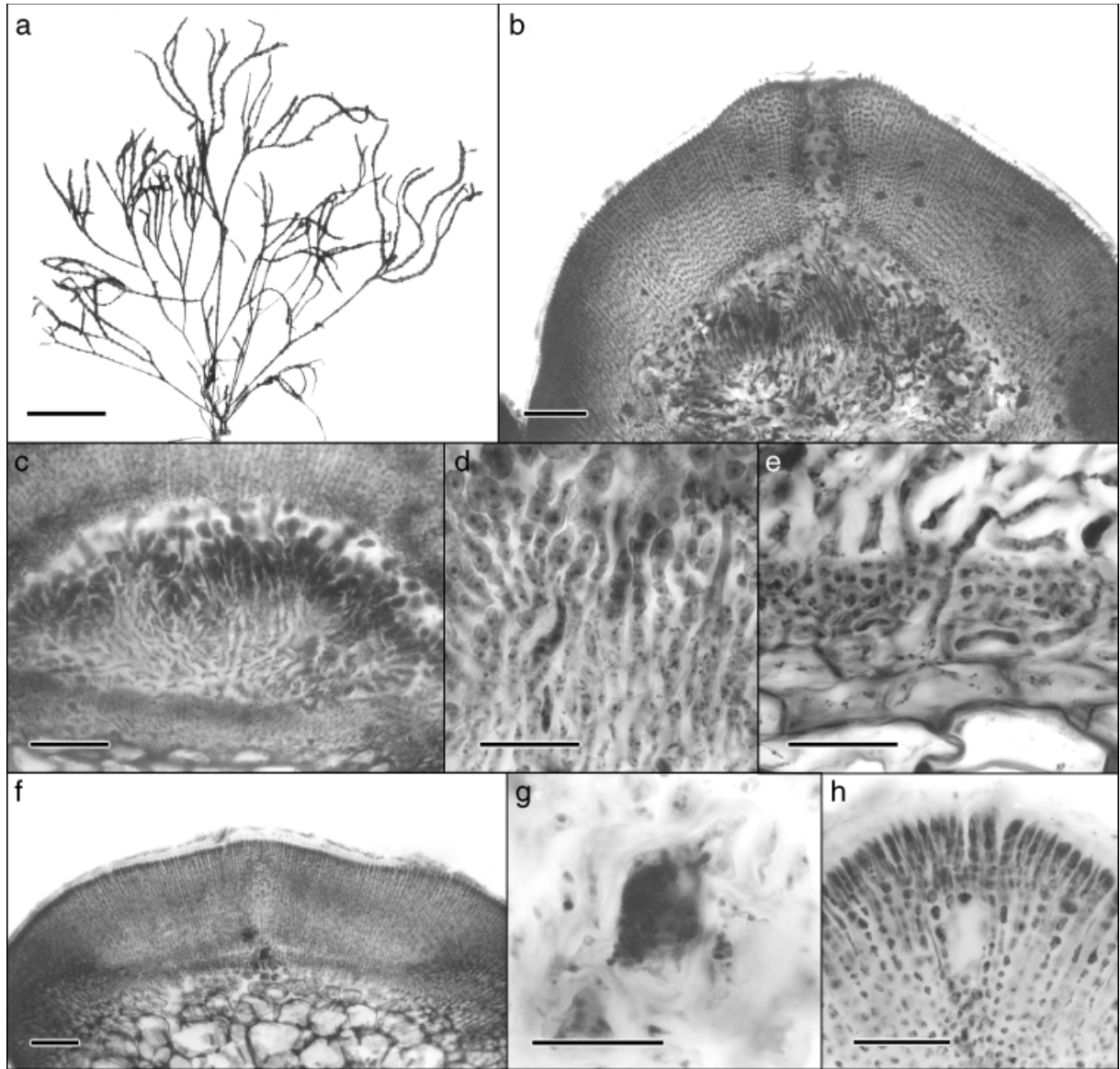


FIG. 10. *Gracilaria aculeata* (Natal, South Africa). (a) Habit of a cystocarpic plant. Scale, 5 cm. (b) Median section of cystocarp and ostiole. Scale, 200  $\mu$ m. (c) Gonimoblasts composed of elongated cells, carposporangial chains, and tubular cells connecting to cells of outer pericarp. (Note the absence of tubular fusion cells.) Scale, 200  $\mu$ m. (d) Close-up of filamentous gonimoblasts, carposporangial chains, and tubular cells. Scale, 100  $\mu$ m. (e) Tubular cells penetrating and fusing with cells of the inner pericarp to form a fusion network. Scale, 100  $\mu$ m. (f) Young cystocarp with a thick pericarp showing the initiation of the ostiole and cystocarp cavity. Scale, 200  $\mu$ m. (g) Optical section of the carpogonial fusion cell visible in f. Scale, 50  $\mu$ m. (h) Initiation of ostiole in the mid-region of the outer pericarp. Scale, 100  $\mu$ m.

(additional references: Bird et al. [1990], Ryan and Nelson [1991], Nelson and Ryan [1991])

*Holotype*: a female plant at National Research Council, Halifax, Canada (NRCC) 9131(a).

*Type locality*: Penco, Bahía Concepción, Prov. Bio-Bio, Chile.

*Specimens examined*: Isla Mancera, Bahía Coral, Prov. Valdivia, Chile.

*Supplementary description*: gonimoblasts composed of isodiametric, uniformly vacuolate cells intercon-

ected by primary and secondary pit connections and bearing carposporangia in straight chains branched only at the bases (Fig. 11a); cells in floor of cystocarp stretched periclinally in a V-shaped arrangement; outer pericarp with cells little modified and with a central ostiole; gonimoblasts attached to cells in floor of cystocarp by tubular cells that issue from inner gonimoblast cells and fuse with individual gametophytic cells beginning in the vicinity of the fusion cell and progressing outwardly as the cystocarp grows in diameter (Fig. 11, a and b); pericarp fusion cells absent.



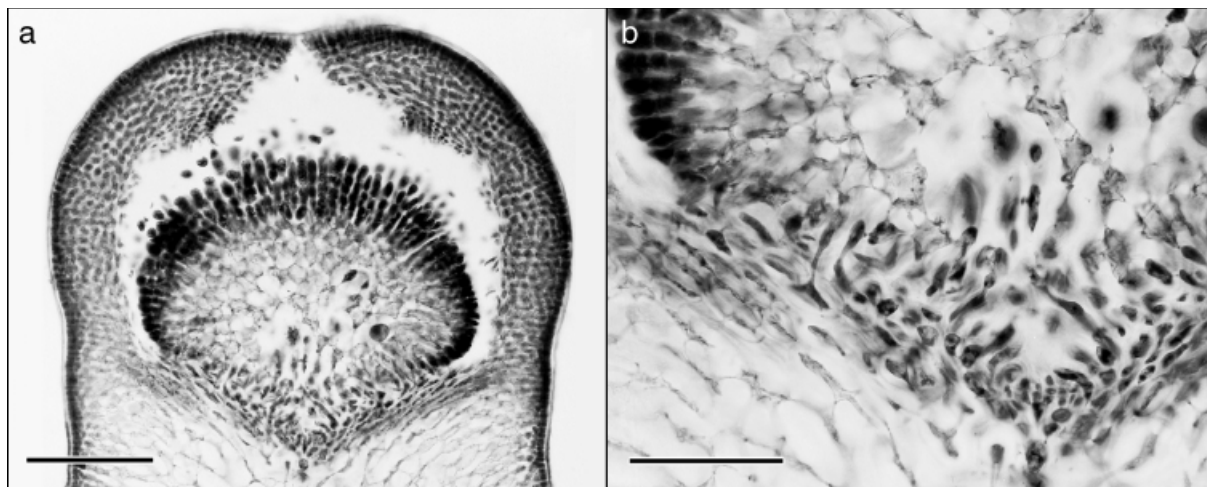


FIG. 11. *Gracilaria chilensis* (Prov. Valdivia, Chile). (a) Median section of a mature cystocarp with ostiole showing vacuolate inner gonimoblasts bearing carposporangial chains. Scale, 200  $\mu$ m. (b) Close-up of basal portion of cystocarp in a showing the reticulate arrangement of the vacuolate inner gonimoblast cells and tubular cells fusing to cells in floor of cystocarp. There is a space where the carpogonial fusion cell would normally be present. Scale, 100  $\mu$ m.

#### DISCUSSION

*Vegetative characters.* Features of vegetative development have not been compared systematically among species of the Gracilariaceae. Apical growth is thought to be multi-axial, but studies suggest that at least some species may be fundamentally uniaxial (Kling and Bodard 1986, Kling et. al. 1989, Fredericq and Hommersand 1989a,b). The compactness or looseness of the medulla and cortex, the sizes and shapes of medullary and cortical cells, and the sharpness of the boundary between the cortex and medulla have sometimes been used for separating species but the application of these characters has been inconsistent.

The morphology of hair-producing cells is a vegetative character that is often overlooked but may be significant, at least at the species level. Hair formation was described by Sjoestedt (1926) for *Gracilaria bursa-pastoris* (as *G. compressa*) and by Rosenvinge (1931) in *Gracilaria gracilis* (Stackhouse) Steen-toft, L. Irvine et Farnham (as *G. verrucosa* [Hudson] Papenfuss), and there have been numerous reports since (Dawson 1949, Umamaheswara Rao 1972, Yamamoto 1978). According to Yamamoto (1978), a hair-cell primordium is a transformed superficial cell that does not differ in size from surrounding vegetative cells in the beginning. It enlarges and produces a protuberance that grows into a hair, after which a constriction takes place at the base of the hair and a pit-connection forms that separates the hair from its subtending cell. The further development and senescence of hair-producing cells has not previously been followed. In this study it was found that the later stages in the development of hair-producing cells varied in different species. In *Gracilaria bursa-pastoris* a hair-producing cell elongates until a transverse concavo-

convex division takes place in the lower third of the cell. A basal cell is cut off and becomes lobed, compressed, and altered cytoplasmically and is eventually incorporated into the cortex. In *G. salicornia*, on the other hand, the entire hair-producing cell is convoluted after the hair is shed, becomes compressed periclinally, and is finally incorporated into the cortex while maintaining its pit connection to the cell below. The two patterns were consistent in plants examined from different geographical regions. Hair-producing cells subtended by basal cells were also observed in *G. urvillei*, but the events that led to septation of the basal cell were not followed.

*Cystocarpic characters.* The Gracilariaceae is distinguished by the presence of a two-celled carpogonial branch borne on a supporting cell that also bears two or more flanking sterile filaments. The carpogonium enlarges after fertilization and fuses with several of the flanking sterile cells to initiate a fusion cell while remaining isolated from the supporting cell by a persistent hypogynous cell. A pericarp is initiated at an early stage consisting of gametophytic filaments that form directly from surface cortical cells in the vicinity of the fertilized carpogonium. Gonimoblasts originate as lobes directly from the carpogonial fusion cell and grow outwardly, surmounted by the developing pericarp (Sjoestedt 1926, Kylin 1930, Fredericq and Hommersand 1989a,b,c, 1990a). At some stage, a cavity develops in the cystocarp by the separation or breakdown of pericarp filaments and a central ostiole forms directly above the fertilized carpogonium.

Hommersand and Fredericq (1990) proposed a model to account for the functional relationship between the diploid carposporophyte and haploid gametophyte generations that recognized three compartments: 1) a photosynthetic gametophytic compart-

ment, 2) a modified inner gametophytic compartment that may process the metabolites of photosynthesis, and 3) the developing carposporophyte. In the Gracilariaceae, the photosynthetic compartment is the outer pericarp, the metabolite-processing compartment is the inner pericarp and associated cortex at the base of the cystocarp, and the carposporophyte corresponds to gonimoblasts that develop from the carpogonial fusion cell after fertilization. Phylogenetic lines that correspond to taxonomic units are recognizable based on the different ways in which the three compartments are modified and utilized.

The structure of the outer pericarp is essentially uniform in all Gracilariaceae. It consists of filaments that grow outwardly from surface cortical cells with infrequent branching and with neighboring cells in separate filaments connected laterally by secondary pit connections. The inner pericarp and associated cortical cells are specially modified in that they contain an increased number of nuclei or the nuclei enlarge, or both, and the cells become more densely filled with cytoplasm during early stages of cystocarp development. A critical distinction between taxa arises in the way in which the developing gonimoblasts link to and interact with the two gametophytic compartments. The genus *Gracilariopsis* is unique among Gracilariaceae in that, except for the carpogonial fusion cell, linkage between gonimoblast cells and gametophytic cells always involves the formation of secondary pit connections (Fredericq and Hommersand 1989b). The carpogonial fusion cell incorporates a limited number of adjoining cells and its remnant in mature cystocarps is small and compressed. Linkage between the gonimoblasts and the floor of the cystocarp by secondary pit connections begins in the vicinity of the fusion cell and progresses circumferentially as the cystocarp increases in size. Basal gonimoblast cells may elongate and penetrate between cells of the inner pericarp, but even these elongated cells cut off conjunct cells that form secondary pit connections with gametophytic cells (Gurgel et al. 2003).

In all other Gracilariaceae, the gonimoblast cells link to gametophytic cells either directly through cell fusion or by means of tubular cells that fuse at their tips with gametophytic cells. Tubular cells are poorly understood structures, and there has been much speculation as to their function. Dawson (1949) called them "nutritive filaments" based on the observation that gonimoblast cells often become vacuolate in mature cystocarps that possess them. Kraft (1977) suggested the name "traversing filaments" as a purely descriptive term that did not imply any particular function, and this name has been adopted by Abbott et al. (1991), Zhang and Xia (1994), Xia and Zhang (1999), and others. Fredericq and Hommersand (1989a) called them "tubular nutritive cells." Fredericq and Norris (1985) and Abbott et al. (1991) traced the history of the names used by different authors. The term "tubular cell" was first proposed by Sjoestedt (1926) and is used here as a descriptive term to refer to a multinucleate

cell that originates within the gonimoblasts and extends and fuses with one or more gametophytic cells in the pericarp or floor of the cystocarp. Fusion of a tubular cell to a gametophytic cell may be a final step in the attachment, and only a single gametophytic cell may be involved. In many cases, however, the first cell to be contacted will fuse with adjoining cells to form an additional fusion product, or fusion cell, within the gametophytic tissues. Depending on the direction of secondary fusion and the number of cells involved, the resulting fusion cell may be an unbranched tubular structure with or without knobs, a forked or highly branched dendritic fusion cell, or a complex fusion network. The form of the gametophytic fusion cell or fusion network in the top, sides, or base of the outer pericarp or in the inner pericarp or cystocarp floor may be diagnostic for species in the Gracilariaceae.

Tubular cells are absent in *Curdia* and *Melanthalia* (Fredericq and Hommersand 1989c, 1990a). An inner pericarp is well differentiated, and gonimoblast cells fuse directly with cells of the inner pericarp without the formation of secondary pit connections. An extensive fusion network is produced in the inner pericarp in *Curdia* in which fusion takes place along side the broadened pit connections (Fredericq and Hommersand 1990a).

In *Gracilaria chilensis* the first tubular cells originate from gonimoblast cells in the vicinity of the carpogonial fusion cell and link directly with inner pericarp cells or cortical cells. New tubular cells are added at the margin as the cystocarp enlarges across a V-shaped base and are especially prominent along the edge at the junction of the gonimoblast base and the gametophytic pericarp (Bird et al. 1990). The multinucleate gametophytic cells enlarge, become deeply staining, and are interconnected by prominent pit connections in the vicinity of the attached tubular cells (Nelson and Ryan 1991). Gametophytic cells that have been contacted by gonimoblast tubular cells evidently do not fuse with neighboring cells, and no additional gametophytic fusion cells are formed.

The most elaborate gametophytic fusion structures are usually found in the cystocarp floor. Short tubular cells emanate from inner gonimoblast cells and attach to inner pericarp cells and cells at the base of the outer pericarp in *G. edulis*. Attachment of the tubular cells is followed by progressive fusion of gametophytic cells to form a fusion network consisting largely of stellate cells in the bowl-shaped base of the cystocarp. The same structures have been illustrated for *Gracilaria subtilis* (Xia et Abbott) Xia et Abbott in Abbott et al. (1991) by Xia and Abbott (1985, as *Polycavernosa* sp.). Forked to highly branched fusion cells are produced in the cystocarp floor in *Gracilaria crassissima* P. et H. Crouan (Fredericq and Norris 1985, Fredericq and Hommersand 1990b) and *G. birdiae* Plastino et Oliveira (2002). In contrast to *G. edulis*, the floor of the cystocarp is flat instead of being concave, and the gametophytic fusion cells are dendritic instead of forming a network.

In large numbers of species of *Gracilaria*, tubular cells unite with cells of both the inner and outer pericarp compartments or just with cells of the outer pericarp. Once a pericarp cell has been contacted by a tubular cell and fused with it, adjoining pericarp cells may be incorporated as fusion progresses from cell to cell, probably by the dissolution of pit connections. Fusion that takes place along a pericarp filament by breakdown of primary pit connections produces a tube-shaped fusion cell. The lateral incorporation of cells in adjacent filaments by breakdown of secondary pit connections produces irregularities, knobs, or sometimes club-shaped fusion cells within the pericarp. Because fusion cells that form at the ends of tubular cells in the outer pericarp are usually tubular in shape, we sometimes call such cell a "tubular fusion cell." In the past, such tubular fusion cells have been confused with the simple tubular cells. They differ, however, in that they are not single multinucleate gonimoblast cells but are the product of the fusion of several to many gametophytic cells that have fused after contact by a gonimoblast tubular cell.

In *Gracilaria urvillei* the gonimoblasts fill the cystocarp cavity and the tubular cells are comparatively short. Long tubular fusion cells are formed in both the outer and laterobasal pericarp as a result of fusion of pericarp cells in straight or oblique series. A similar condition is seen in *G. eucheumatoides* except that the gametophytic fusion cells may have lateral knobs or be forked. In *Gracilaria caudata* J. Agardh (Plastino and Oliveira 1997), simple or branched fusion cells are formed in the inner pericarp and tubular cells and, perhaps, tubular fusion cells are produced in the outer pericarp. Inner gonimoblast cells link to cells of the inner pericarp to form an extensive tubular network in *Gracilaria aculeata*, whereas abundant tubular cells connect to the innermost cells of the outer pericarp and tubular fusion cells are absent. A mixed pattern is seen in *G. salicornia* in which tubular cells that have attached to cells of the lower lateral pericarp give rise to branched or dendritic fusion cells and those that link to cells of the outer pericarp produce tubular fusion cells.

In *Gracilaria bursa-pastoris* and *G. beckeri* the tubular cells unite with cells in the outer pericarp followed by progressive fusion of pericarp cells to form prominent tubular fusion cells. The presence of remnant pit connections along the length of a tubular fusion cell is striking evidence for a process that incorporates some pericarp cells and not others. Some species possess elaborate club-shaped tubular fusion cells, for example, the one illustrated by Dawson (1949, pl. 7, fig. 4) in *Gracilaria subsecundata* Setchell et Gardner. A few short tubular cells may also connect inner gonimoblast cells with cells of the inner pericarp, perhaps as a remnant condition. Gargiulo et al. (1992, fig. 26A) illustrated this behavior in *G. bursa-pastoris*.

The cellular make-up of the central sterile gonimoblast region has sometimes been used to distinguish species, although Bird and McLachlan (1984) noted that cellular changes sometimes result from aging and

improper preservation techniques. They observed large protoplasmic gonimoblast cells in *Gracilaria multipartita* (Clemente) Harvey (as *G. foliifera* [Forsskål] Børgesen) from England that turned progressively vacuolate and filamentous as their nutritive function was seemingly replaced by the tubular cells. Cells of the sterile inner gonimoblasts are large and pseudoparenchymatous in *G. chilensis*, *G. salicornia*, *G. edulis*, and *G. eucheumatoides*. They are elongate, filamentous, and not as highly vacuolate in *G. aculeata*, *G. bursa-pastoris*, and *G. beckeri*. The pseudoparenchymatous condition of gonimoblasts seen in young stages in *G. edulis* and *G. eucheumatoides* persists in mature cystocarps.

Carposporangia are borne in chains at the periphery of the sterile gonimoblasts in species of Gracilariaceae. Carposporangial chains are straight and largely unbranched in *Melanthalia* and *Curdiea* with the carposporangia maturing basipetally. New filaments are interpolated by intercalary divisions of gonimoblast cells deep inside the fertile region (Fredericq and Hommersand 1989c, 1990a). The mature gonimoblasts of *Gracilaria chilensis* are strikingly similar to those of *Gracilariopsis* (Fredericq and Hommersand 1989b) in which basally branched straight carposporangial chains of uniform length are borne on the periphery of a vacuolate sterile inner gonimoblast mass. A similar condition occurs in *G. edulis* and *G. urvillei*; however, the carposporangial filaments in many species are more highly branched or form clusters, as in *G. gracilis* (Fredericq and Hommersand 1989a, figs. 30–35, as *G. verrucosa*).

The cystocarp cavity may develop in one of several ways. Withell et al. (1994) illustrated the progressive formation of a large hemispherical cavity by the dissolution of pericarp cells in *Gracilaria cliftonii* Withell, Millar et Kraft and *G. stipitata* Withell, Millar et Kraft. A similar pattern is seen here in *G. edulis*. Alternatively, filament separation may occur across a plane between the pericarp and the cystocarp floor or within the developing pericarp itself. Dissolution between filaments in a developing pericarp, seemingly as a result of the breakdown of primary pit connections, splits the pericarp into inner and outer layers. The resulting inner layer has commonly been referred to as an inner pericarp. When the separation takes place between pericarp cells and cells in the floor of the cystocarp, an inner pericarp is said to be absent. Often the distinction between the two types is obscure. For example, Fredericq and Hommersand (1989b) described a condition in which darkly staining cells contain large nuclei at the base of the cystocarp cavity, which they referred to as "inner pericarp" in *Gracilariopsis*. Some of these cells may indeed correspond to basal cells of pericarp filaments, but others may be vegetative cells of the inner cortex. Among the species studied here, an inner pericarp is prominent in *G. bursa-pastoris*, *G. aculeata*, and *G. salicornia* but is obscure in *G. urvillei*, *G. edulis*, *G. eucheumatoides*, and *G. beckeri*. The cystocarp cavity forms by separation between inner and outer pericarp layers at an early stage of gonimoblast

development and spreads across the cystocarp floor to produce a broad cystocarp cavity in *Gracilaria aculeata* and in *G. cornea* J. Agardh (Fredericq and Norris 1985, as *G. debilis* [Forsskål] Børgesen), *G. crassissima* (Fredericq and Hommersand 1990b), and *G. birdiae* Plastino et Oliveira (Plastino and Oliveira 2002).

The size, shape, and arrangement of cells in the pericarp may provide useful characters for distinguishing species of *Gracilaria* (Chiang 1985, Xia 1985, Xia and Abbott 1987, figs. 10–14, as *Polycavernosa*). In *G. euchematoides*, the pericarp cells are of uniform size in young cystocarps with a band of darkly staining cells in the mid-region and a basal layer of cells with enlarged nuclei. Once the cystocarp matures, these distinctions disappear. It is likely that differences in staining properties reflect different physiological states that may be correlated with age. Cell shape may also change in response to patterns of cystocarp expansion. Pericarp cells can stretch laterally, as in *G. salicornia*, *G. urvillei*, and *G. euchematoides*. Alternatively, they may separate into fascicles due to breakdown of lateral pit connections, as in *G. edulis*. Other features such as cell wall thickness and cell shape within the pericarp have been discussed by Xia and Abbott (1987), who have speculated regarding the usefulness of these characters in species taxonomy.

Although many cystocarp characters are highly variable, features that reflect nutritional strategies undergo directional changes that may have phylogenetic significance. We recognize the following progression: 1) from small fusion cells with few incorporated vegetative cells to large fusion cells with many incorporated vegetative cells; 2) from enlarged pit connections between gonimoblast and gametophyte cells, without fusion, to cell fusion between gonimoblast and gametophyte cells; 3) from fusion cells or fusion networks present only the inner pericarp and floor of the cystocarp to fusion structures present in both the inner and outer pericarps; 4) from condition 3 to tubular cells and tubular fusion cells present in the outer pericarp and absent or greatly reduced in the inner pericarp.

*Spermatangial characters.* Several authorities (Dawson 1949, 1961, Børgesen 1953, Ohmi 1958a,b) have stressed the importance of spermatangial morphology in the taxonomy of *Gracilaria*. Yamamoto (1975) described three types of spermatangial configuration in *Gracilaria*: 1) chorda type, represented by *Gracilaria chorda* Holmes, in which spermatangial parent cells are produced from outer cortical cells and divide transversely to form a continuous superficial layer of spermatangia; 2) textorii type, represented by *Gracilaria textorii* (Suringar) Hariot, in which outer cortical cells are transformed into spermatangial parent cells that divide to form branches lining a shallow sorus flanked by narrow, elongate cortical cells; and 3) verrucosa type, represented by *Gracilaria verrucosa* (Hudson) Papenfuss, in which spermatangial parent cells are generated in extensive filaments that originate from intercalary cortical cells and line the

intercellular space, forming a deep pot-shaped conceptacle with spermatangia covering its entire inner surface. Yamamoto (1975) established three subgenera within *Gracilaria* based on the three spermatangial types: subgenus *Gracilariella* with chorda-type spermatangia, subgenus *Textoriella* with textorii-type spermatangia, and subgenus *Gracilaria* with verrucosa-type spermatangia.

Børgesen (1953) documented a distinct spermatangial type characterized by the presence of “small globular caves ... the interior of which become divided into a number of small compartments from the wall of which small bodies like antheridia are developed” in a new species from Mauritius, *Gracilaria multifurcata* Børgesen. He hesitated to call these structures antheridial bodies because he could not find any ostioles to the outside. Similar globular bodies were reported by Ohmi (1958a) in *Gracilaria henriquesiana* Hariot from the coast of Ghana. He referred to these as antheridial conceptacles, although, like Børgesen, he did not find an aperture through which spermatia might exit. Chang and Xia (1963) recognized the special nature of the compartmental spermatangial conceptacles and erected a new genus, *Polycavernosa* Chang et Xia, to accommodate plants from southern China that possessed them. In addition, they documented the presence of band-like, branched, basal, nutritive filaments issuing from the innermost gonimoblasts that traversed into the base of the cystocarp and the absence of similar filaments between the gonimoblasts and the pericarp. Yamamoto (1984) expanded his classification of spermatangial types to five including the Symetrica type, with discontinuously superficial spermatangia, and the Henriquesiana type, with aggregated verrucosa-type conceptacles. Tseng and Xia (1999) proposed the subgenus *Hydropuntia* to accommodate species characterized by the presence of polycavernosa type (equivalent to Henriquesiana type?) spermatangia.

Despite the emphasis placed on spermatangial type in the present classification of species of *Gracilaria*, the developmental patterns that underlie the different types are poorly understood. Fredericq and Hommersand (1989b) reported that in *Gracilariopsis andersonii* (as *G. lemaneiformis*) from California the spermatangia were cut off by oblique longitudinal divisions from uninucleate spermatangial parent cells in the outer cortical layer. This was confirmed by Bouzon et al. (2000), except to say that in some cases the spermatangial parent cell may originate from a subterminal cortical cell in *Gracilariopsis tenuifrons* (Bird et Oliveira) Fredericq et Hommersand. Fredericq and Norris (1992) illustrated a sequence in the shallow textorii-type spermatangial conceptacle of *Gracilaria blodgettii* Harvey in which an outer cortical cell produced a series of spermatangial parent cells leading to the establishment of a spermatangial sorus. Only rarely was a subcortical cell generative in *G. blodgettii*. On the other hand, Bouzon et al. (2000) showed that a subterminal intercalary cell proliferates in an ordinate sequence in

*G. mamillaris* to produce a textorii-type conceptacle. A textorii-type spermatangial conceptacle has been described in *Gracilaria chilensis* by Ryan and Nelson (1991, as *G. sordida*) in which spermatangia are produced basipetally in succession from each spermatangial parent cell. Fredericq and Hommersand (1989a) described a process in *G. gracilis* (as *G. verrucosa*) in which a single subcortical cell gave rise to a branched filamentous system that produced spermatangial parent cells and spermatangia that lined deep verrucosa-type conceptacles. When Xia and Abbott (1985) put forward a list of reproductive characters supporting the recognition of the genus *Polycavernosa*, they emphasized the intercalary (= subcortical) origin of its multicavitated spermatangial conceptacles. Now that an intercalary origin of spermatangial filaments has been seen in all types of spermatangial conceptacles, the multicavitated form can no longer be considered unique in this regard. Bouzon et al. (2000) expressed the opinion that the wide variation in conceptacle organization in *Gracilaria*, commonly described as "polycavernosa," "verrucosa," and "textorii" types are simply extremes in a morphological continuum. They suggested that these characters should probably not be used to separate supraspecific categories, as had previously been proposed.

Bird and McLachlan (1984) reported compound spermatangial conceptacles in *Gracilaria gracilis* (as *G. verrucosa*) and recommended caution in interpreting the compound conceptacles in *Polycavernosa* (Bird 1995). Abbott et al. (1991) found spermatangial plants that showed both verrucosa- and polycavernosa-type conceptacles in *Gracilaria mixta* Abbott, Zhang et Xia and *G. changii* (Xia et Abbott) Abbott, Zhang et Xia. Verrucosa-type conceptacles were confined to the distal portion of a branch approximately 1 cm from the apex, became mixed with polycavernosa type at approximately 3 cm, and were finally replaced with only polycavernosa-type conceptacles at 4.5 cm from the tips. Similarly, we observed verrucosa-like young stages in the ontogeny of the polycavernosa-type conceptacles of *Gracilaria urvillei*. The multicavitated conceptacles of *G. edulis* are each provided with a single bulging external opening covered by a cuticle. Early stages of conceptacle formation in *G. urvillei* and *G. edulis* show outpocketing associated with elongation of surrounding cortical and medullary cells, a feature that continues as the conceptacles expand and become multicavitated. Similar elongate thin-walled cells are reported surrounding the verrucosa- and polycavernosa-type conceptacles in *Gracilaria harveyana* J. Agardh from Australia (Withell et al. 1994). In contrast, the conceptacles of *G. salicornia* are symmetrically urn shaped, appear to have a stable configuration, and remain separate from adjacent conceptacles. A multicavitated male conceptacle that begins as a single cavity may extend in some incompletely known way at the same time that spermatangial filaments grow and branch within the extended cavity. Alternatively, polycavernosa-type conceptacles, like the ones found in

*Gracilaria harveyana*, *G. mixta*, and *G. changii*, may have arisen through fusion of simple conceptacles in the course of their ontogeny. Spermatangial parent cells link to vegetative cells by secondary pit connections in the multicavitated conceptacles of *Gracilaria crassissima* (Fredericq and Hommersand 1990b, fig. 14). At the present time there is no evidence of secondary pit connections of this type in *G. edulis* or *G. urvillei*.

Species reported as having textorii-type conceptacles may be surrounded by elongated cortical flanking cells, as in *G. chilensis* (Bird et al. 1986, fig. 6; 1990, figs. 1, 2), or flanking cells may be absent, as in *G. blodgettii* from Florida (Fredericq and Norris 1992). The textorii-type conceptacle with narrow flanking cortical cells originally described by Yamamoto (1975) and the shallow pit-like conceptacles without flanking cortical cells observed by Fredericq and Norris (1992) and others (Dawson 1949, Umamaheswara Rao 1972) may represent two distinct spermatangial types. Bird and McLachlan (1982), Yamamoto (1984), and Bird (1995) discussed the types of spermatangial conceptacles known in *Gracilaria*. It seems likely that taxonomically significant differences have gone unrecognized among all the variations seen and imperfectly understood.

*Tetrasporangial characters.* Tetrasporangial configuration has been used to differentiate genera in the Gracilariaceae. Tetrasporangia may be distributed more or less continuously over the fertile thallus, may be localized in sori, or may form raised structures referred to as nemathecia. Three tetrasporangial cortex types may be recognized in longitudinal and cross-sections: 1) an unmodified cortex generally without associated elongated cells or with narrow cells present only adjacent to the tetrasporangia, as in *Gracilaria edulis*; 2) a filamentous cortex of elongated cells that does not extend above the thallus surface, as in *G. urvillei*; and 3) a cortex composed of elongated cells that extend above the thallus surface producing a nemathecium, as in *G. beckeri*. This last type is easy to identify with the naked eye, because nemathecia cause swellings on the surface accompanied by a coloration change compared with that of surrounding sterile tissue. An unmodified cortex seems to be the most common type found in *Gracilaria*. Dawson (1949) documented a variety of tetrasporangial types ranging from those with "little modified cortex of anticlinally oblong cells," as in *G. spinigera* Dawson to "well and conspicuously developed nemathecia" in *G. textorii* (as *G. vivesii* Howe). The genera *Curdiea* and *Melanthalia* are characterized by cruciate tetrasporangia produced within nemathecia in which each unit consists of a bearing cell and an elongated tetrasporangium surrounded by raised cortical filaments (Fredericq and Hommersand 1989c, 1990a). The genus *Tyleiophora* (*Gracilaria beckeri*) was established solely on the basis of the presence of raised tetrasporangial nemathecia, a feature confirmed in this study.

## TAXONOMIC CONCLUSIONS

The taxonomic history of the Gracilariaceae has been one in which new genera and subgenera have been established based on a single character, only to see the species later returned to *Gracilaria* when more taxa had been studied and it was shown that the key character did not define a natural group. Thus, the nineteenth century genera *Corallopsis* Greville (1830, axes constricted), *Hydropuntia* Montagne (1842, spiny axes with constrictions at the nodes), and *Tyleiophora* J. Agardh (1890, nemathecial tetrasporangia, all fell into disuse as unrelated species were discovered that shared in these characters.

The same fate befell the twentieth century genus *Gracilariopsis* Dawson (1949, tubular cells absent from the cystocarp) when species exhibiting this character were found to possess either superficial spermatangia or spermatangia borne in deep cavities. Likewise, *Polycavernosa* Chang and Xia (1963, multichambered spermatangial cavities) was rejected when this character was found to show gradation and to be associated with a variety of types of cystocarps. Although the spermatangial types recognized by Yamamoto (1975, 1978, 1984) are applied almost universally in descriptions of *Gracilaria* species, the subgenera *Gracilaria*, *Gracilariella*, and *Textoriella* that he proposed are seldom recognized, again because spermatangial type is not consistently correlated with any other taxonomic character (Bird 1995).

Groups of species are identified in this study that exhibit spermatangial types associated with particular patterns of cystocarp development. In the absence of a comprehensive monograph of the Gracilariaceae, these groups are small and their inclusiveness is unknown. In the course of time, some may be recognized as genera or subgenera. Here we designate each group by a representative species listing published generic names where these may apply. Species groups listed in Table 1 are as follows: 1) abscissa group (*Melanthalia*), 2) flabellata group (*Curdiea*), 3) lemaneiformis group (*Gracilariopsis*), 4) chilensis group, 5) edulis group (*Plocaria*, *Polycavernosa*), 6) urvillei group (*Hydropuntia*), 7) crassissima group, 8) salicornia group (*Corallopsis*), 9) gracilis group, and 10) bursa-pastoris group (*Gracilaria*).

The type species of *Gracilariophila* and *Congracilaria* are adelphoparasites that are closely related to their host species (Fredericq et al. 1989, Goff and Zuccarello 1994, Terada et al. 1999). The taxonomic status of the poorly known genus *Gracilariocolax* Weber van-Bosse (1928) remains in doubt; however, see Terada et al. (1999) and Gerung et al. (1999). Parasitic genera are not part of the history of *Gracilaria* and are excluded from the treatment below.

1. Abscissa group (*Melanthalia*). *Melanthalia* is thought to have retained the ancestral pattern of vegetative and reproductive development in the Gracilariaceae. The thallus possesses a dome-shaped apex composed of long filaments in which the

formation of secondary pit connections between cells in separate cell rows is delayed (Papenfuss 1935, Fredericq and Hommersand 1990a). Spermatangia have not been illustrated but are thought to be superficial (Womersley 1996). Cystocarps of *Melanthalia* are massive with the early formation of radiating files of pericarp filaments from surface cortical cells at a time when the carpogonial fusion cell is still small. The gonimoblasts are composed of files of cells that extend radially and branch by intercalary cell divisions. Gonimoblast cells are densely filled with cytoplasm, and lateral secondary pit connections arise at a distance behind the apex. A cystocarp cavity forms around the developing gonimoblasts and becomes readily distinguishable only after carpospore initiation. Cells of the inner pericarp are multinucleate with conspicuous enlarged nuclei and lower gonimoblast cells fuse directly with cells of the inner pericarp in apparent nutritional support of the gonimoblasts and developing carposporangial chains. Tetrasporangia are borne in nemathecium with the tetrasporangia terminal, flanked by compressed lateral filaments in which secondary pit connections are absent (Fredericq and Hommersand 1990a). The genus *Melanthalia* is well established and presently includes six species from Australia, New Zealand, and New Caledonia (Womersley 1996).

2. Flabellata group (*Curdiea*). The vegetative tip of *Curdiea* is more advanced than that of *Melanthalia* in that secondary pit connections are initiated close to the apex. Male plants produce spermatangia in nemathecium in which cells of the cortex undergo a series of oblique longitudinal divisions by means of concavo-convex septa to produce clusters of spermatangial parent cells covered by a thick outer wall that lifts off at the time of spermatial release (Nelson and Knight 1997). Gonimoblasts and carposporangia are arranged in radial rows, and the cystocarp cavity forms directly above the gonimoblasts as in *Melanthalia*. The cells of the inner pericarp contain even larger nuclei than in *Melanthalia*. Fusions between inner gonimoblast cells and inner pericarp cells are prominent, and a fusion network is formed in which inner pericarp cells fuse alongside persistent pit connections (Fredericq and Hommersand 1989c). Tetrasporangia are borne in nemathecium covered by a thick outer wall and form terminally by concavo-convex division of surface cortical cells. Like *Melanthalia*, *Curdiea* is well established and presently includes seven species from Australia and New Zealand and one distantly related species from Antarctica and the Subantarctic Islands (Womersley 1996).

3. Lemaneiformis group (*Gracilariopsis*). *Gracilariopsis* is cylindrical with a dome-shaped apex that is less massive than that of *Melanthalia*. Spermatangia are superficial, derived singly or in small clusters from surface cortical cells. Gonimoblasts are initiated from a small fusion cell that becomes compressed or is evanescent at maturity. Inner pericarp cells are strongly differentiated and consist of multinucleate cells with enlarged nuclei. The innermost gonimoblast

cells sometimes elongate and penetrate between inner pericarp cells but do not fuse directly with them. Instead, they cut off small conjuctor cells that fuse with cells of the inner pericarp forming secondary pit connections. Gonimoblast filaments branch monopodially, interconnect by secondary pit connections, and bear carposporangia in basally branched straight chains. The cystocarp cavity forms above the developing gonimoblasts and extends laterally at the margins by the breakdown of pit connections between files of inner and outer pericarp cells. Linkage between the gonimoblasts and inner pericarp, which began in the vicinity of the fusion cell, extend laterally to form a broad base across the floor of the cystocarp. Tetrasporangia are produced by oblique divisions from surface cells and are never nemathecial (Fredericq and Hommersand 1989b, Gurgel et al. 2003). *Gracilariopsis* presently contains seven species worldwide and is undergoing extensive taxonomic revision (Gurgel et al. 2003).

4. Chilensis group. Thalli are cylindrical and similar in habit to species of *Gracilariopsis*. Spermatangia are borne in shallow conceptacles bordered by tall flanking cortical cells. The cystocarp superficially resembles that of *Gracilariopsis lemaneiformis*. As with *G. lemaneiformis*, the fusion cell is compressed or evanescent in mature cystocarps. Instead of cutting off conjuctor cells, the inner gonimoblast cells link to inner pericarp cells through direct fusion or by means of short or long multinucleate tubular cells. The base of an expanding cystocarp is V shaped rather than flat, and inner pericarp cells are contacted progressively at the base as the cystocarp expands. Mature inner gonimoblast cells are isodiametric and interconnect by numerous secondary pit connections. Carposporangia are borne in straight chains at the periphery of the gonimoblasts, as in *Gracilariopsis*. Tetrasporangia are superficial and scattered throughout the cortex. *Gracilaria chilensis* is widely distributed in the Southern Hemisphere from Chile, New Zealand (Bird et al. 1990), southern Australia, and Tasmania (Byrne et al. 2002) A second species, *Gracilaria tenuistipitata*, is reported from East Asia (Xia and Zhang 1999) and may be widely distributed in the Northern Hemisphere.

5. Edulis group (*Plocaria*, *Polycavernosa*). Thalli are mostly cylindrical or compressed. Spermatangial conceptacles are multicavities, formed by separation of inner cortical cells permitting the spermatangial filaments to line the dissected cavity, apparently without the formation secondary pit connections. Typically, there is only one ostiole. As in *G. chilensis*, the inner gonimoblast cells link to inner pericarp cells in the floor of the cystocarp by direct fusion or by means of tubular cells. The chief distinction is that the contacted pericarp cells fuse with one another to form a reticulate network that stains readily with hematoxylin or aniline blue. Inner gonimoblast filaments are isodiametric, linked by numerous secondary pit connections, and the carposporangia are borne in short branched chains around the periphery of the gonimoblasts. The cystocarp cavity

opens above the developing gonimoblasts by the lateral separation of pericarp filaments, as in *G. chilensis*. Tetrasporangia are unspecialized and are scattered among the surface cortical cells. At the present time the edulis group is represented chiefly by *Gracilaria edulis*, *G. subtilis* (Abbott et al. 1991), and plants referred to incorrectly as *G. coronopifolia* (Gerund et al. 1999) in the Indo-West Pacific Ocean. *Gracilaria preissiana* (Sonder) Womersley and *G. perplexa* Byrne et Zuccarello (Byrne et al. 2002) from Australia also belong to this group.

6. Urvillei group (*Hydropuntia*). Thalli are terete to compressed with constricted nodes or constrictions at the bases of branches. Withell et al. (1994) illustrated a multicavities conceptacle for *G. urvillei* that is strikingly similar to that found in *G. edulis*; however, our observations suggest that the multicavities conceptacles may arise, in part, from conceptacle fusion. The gonimoblasts completely fill the cystocarp cavity with darkly staining elongate inner gonimoblast filaments bearing peripheral clusters of carposporangia in short branched chains. Tubular cells link to cells at the base of the pericarp that lead to the formation of simple or branched pericarp fusion cells. Unlike *G. edulis*, tubular cells also contact cells in the outer pericarp, which unite to form tubular fusion cells in straight or oblique series. The pericarp is initially differentiated cytologically into light- and dark-staining layers. Tetrasporangia are elongate and deeply embedded in the thallus surrounded by files of cortical filaments. As circumscribed here, the urvillei group contains only *Gracilaria urvillei* and *G. eucheumatoides* from the Indo-West Pacific Ocean.

7. Crassissima group. Thalli are cylindrical to slightly compressed. Spermatangial conceptacles are multicavities, and their formation may involve lateral extensions and secondary fusion. The spermatangial filaments link to cortical and medullary cells by secondary pit connections, a feature that may be diagnostic for the group. Gonimoblasts develop from a large highly ramified fusion cell. The cystocarp cavity originates schizogously lateral to the fusion cell separating the pericarp into prominent inner and outer layers. As the gonimoblasts grow, they spread across the inner pericarp layer and send down thick tubular cells that link to inner pericarp cells and give rise to branched (dendritic) fusion cells. Cystocarps are broad and flat, and tubular cells connecting to the outer pericarp are absent in most species but present in some. Tetrasporangia originate laterally from cortical cells and are flanked by short filaments (Plastino and Oliveira 2002, and included references). This group includes *Gracilaria crassissima* and *G. cornea* among species that lack tubular cells that connect to the outer pericarp and, possibly, *G. caudata* and *G. birdiae* among species that possess such tubular cells. All are from tropical and warm-temperate regions in the Western Atlantic Ocean.

8. Salicornia group (*Corallopsis*). Members of the salicornia group are terete to compressed, with nodal constrictions or constrictions at the bases of branches.



The group possesses deep individual verrucosa-type spermatangial conceptacles lined by elongated or collapsed cortical cells. Gonimoblasts produce tubular cells that attach to the basal and outer pericarp. The ones that link to the basal pericarp give rise to branched fusion cells, whereas those that contact cells in outer pericarp may give rise to linear tubular fusion cells. The inner pericarp consists of darkly staining cells with enlarged nuclei linked to the fusion cell by broadened pit connections. The cystocarp cavity is formed schizogenously by the breakdown of pit connections between cells of inner and outer pericarp filaments. In addition to *Gracilaria salicornia*, the group contains *G. canaliculata* Sonder, two closely related species from the Indo-West Pacific Ocean (Withell et al. 1994). *Gracilaria aculeata* is more distantly related and is restricted to East Coast of southern Africa.

9. *Gracilis* group. Thalli are terete. Spermatangia of *Gracilaria gracilis* are formed in deep, individual, or fused conceptacles. Branched spermatangial filaments initiated from inner cortical cells line the cavity of the conceptacle but do not link to cortical cells by secondary pit connections. Tubular cells are initiated at an early stage of gonimoblast development that link to cells in the outer pericarp, leading to formation of tubular fusion cells. Cells of the inner pericarp are densely filled with cytoplasm and are progressively incorporated into an expanding fusion cell. Inner gonimoblast cells are isodiametric and vacuolate at maturity and bear carposporangia in clusters of branched chains. The cystocarp cavity forms progressively by separation and dissolution of pericarp filaments above the gonimoblasts. Tetrasporangia are formed from outer cortical cells by oblique divisions (Fredericq and Hommersand 1989a, Steentoft et al. 1995). Species include *G. gracilis* from Atlantic Western Europe, *G. pacifica* from Pacific North America, and *G. vermiculophylla* from Eastern Asia.

10. *Bursa-pastoris* group (*Gracilaria*). The *bursa-pastoris* group comprises a large morphologically diverse assemblage of species, including *Gracilaria beckeri*, the type species of *Tyleiophora* J. Agardh. Two characters distinguish most members of the group at the present time: spermatangia borne in shallow textorii-type conceptacles and gonimoblasts producing tubular cells that link to cells of the outer pericarp with the formation of tubular fusion cells. Tubular filaments that connect to the inner pericarp or cystocarp floor are highly reduced or absent in most species. The type species *Gracilaria compressa* (= *G. bursa-pastoris*) is further distinguished by the presence of a persistent fusion cell and an inner pericarp composed of linear files of cells containing enlarged nuclei. Formation of the cystocarp cavity is schizogenous in this species by the separation of inner and outer pericarp at an early stage of cystocarp development.

The phylogenetic analyses of Bird et al (1992), Bellowin et al. (2002) based on nuclear-encoded small subunit rDNA, and Gurgel and Fredericq (2004) based

on chloroplast-encoded *rbcL* sequences identify three large clades, one of which corresponds to *Melanthalia* and *Curdiea*, one to *Gracilariopsis*, and one to *Gracilaria* sensu lato. Each of the three is also well supported by the morphological evidence. Beyond the three major assemblages, each of the groups recognized here based on morphological criteria received moderate to strong bootstrap support in maximum parsimony and Bayesian likelihood analyses of the *rbcL* data (Gurgel and Fredericq 2003). The basal position of the chilensis group within *Gracilaria* sensu lato was well supported in agreement with the observation that gonimoblast tubular cells link to gametophytic cells without there being any further fusion of gametophytic cells. There was weak support for uniting the *edulis*, *urvillei*, and *crassissima* groups characterized by a multicavitated spermatangial conceptacle and for uniting the *salicornia* and *gracilis* groups characterized by a verrucosa-type spermatangial conceptacle. Gurgel and Fredericq (2003) referred the *edulis* and *urvillei* groups to *Hydropuntia* and proposed that a new genus be established to receive the *crassissima* group. A terminal clade that contained the type species of *Gracilaria*, *G. bursa-pastoris*, received bootstrap support.

New morphological and molecular evidence may ultimately justify the recognition of several genera presently placed in synonymy under *Gracilaria*. When a sufficient number of species have been investigated to permit a revision of the Gracilariaceae, the proposed classification should consider the priority of validly published generic names that apply to the groups presently subsumed under *Gracilaria*.

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