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Taxonomy of *Melanthalia obtusata* var. *abscissa* and its placement in the Gracilariales (Rhodophyta)

Suzanne Fredericq

Department of Botany, National Museum of Natural History, Smithsonian Institution, Washington, USA

Max Hommersand

Department of Biology, University of North Carolina, Chapel Hill, USA

SUMMARY

Melanthalia obtusata var. *abscissa* from New Zealand has been reinvestigated with regard to its reproductive morphology, and the results show that *Melanthalia* is a distinct genus within the Gracilariaceae (Gracilariales). Diagnostic for *Melanthalia* are a prominent dome-shaped apical zone consisting of parallel files of small, dark, cytoplasm-rich, outer cortical cells of uniform size; globule-filled thick-walled vegetative cells; minimal space between the gonimoblast and pericarp (cystocarp cavity); an inner pericarp composed of small, darkly staining multinucleate cells; formation of small fusion centers in the floor of the cystocarp as result of terminal gonimoblast cells fusing directly onto inner pericarp cells, with the fusion products incorporating still additional cells; formation of fusion centers within the hyaline sterile gonimoblast due to fusion of laterally contiguous sterile gonimoblast cells; organization of upper gonimoblast cells into rather straight chains composed of small, round carposporangia; production of tetrasporangia in nemathecia. The generic concept within the Gracilariaceae is reviewed. Of the genera of the Gracilariaceae, the closest taxonomic affinities of *Melanthalia* are wich *Curdiea*.

Introduction

Montagne ([27], p. 296) erected the genus *Melanthalia* based on *Fucus obtusatus* Labillardière. Labillardière ([26], p. 111) had described *F. obtusatus* from Cap van Diemen, New Holland, southern Australia, and provided an illustration of a cystocarpic specimen (plate 255). A few years later, Turner ([29], p. 25, pl. 145) also reported and illustrated *Fucus obtusatus* from New Holland.

C. Agardh ([1], p. 383) transferred *Fucus obtusatus* Labill. to the genus *Rhodomela*, establishing *Rhodomela obtusata* (Labill.) C. Agardh, while Greville ([12], p. lxix) placed *Fucus obtusatus* Labill. in the 'paradoxical and perobscure algae'. J. Agardh ([3], p. 53) viewed *Fucus obtusatus* Labill. as being taxonomically related to *Gracilaria* Greville.

While Montagne [27] designated *Fucus obtusatus* Labill. as the basionym for his new combination, he failed to make the valid combination *Melanthalia obtusata*. Instead, page 298, he provided a superfluous name, *Melanthalia billardieri* Mont., to accomodate *Fucus obtusatus* Labill. Later, J. Agardh ([4], p. 613) made the formal combination *Melanthalia obtusata* (Labill.) J. Agardh. In addition to the type species, Montagne ([26], p. 299) also described *Melanthalia jaubertiana* Mont. without citing where it was collected.

A cystocarpic specimen from the original collection of Labillardière (Figs. 1–2), communicated to Montagne by M. Webb, is deposited in the Montagne Herbarium (PC), and is in all likelihood the specimen Montagne had studied (Ardré, pers. comm., see Montagne [27], p. 297).

Turner ([30], p. 65, pl. 223) described *Fucus abscissus*

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from New Zealand, subsequently transferred to *Sphaerococcus* by C. Agardh ([2], p. 217). Later, Hooker and Harvey [20, p. 548] transferred *Fucus abscissus* to *Melanthalia*, establishing *Melanthalia abscissa* (Turner) Hook. et Harv.

Kützing ([22], p. 784) accepted the generic placements of both *Melanthalia billardieri* Mont. [= *M. obtusata*] and *M. jaubertiana* Mont., but transferred (p. 752) *Fucus abscissus* Turner to *Chondrococcus*, establishing *Chondrococcus abscissus* (Turner) Kützing, a taxonomic move he continued to maintain ([23], p. 29). Two years later, Kützing ([24], Tabs. 42–43) cited both *M. billardieri* Mont. [= *M. obtusata*] and *M. jaubertiana* Mont., and described three new species of *Melanthallia* (*M. vieillardi* and *M. fastigiata* from New Caledonia, and *M. muelleri* from New Holland).

Hooker and Harvey ([20], p. 548) and Harvey ([13], p. 444) did not view *M. abscissa* and *M. jaubertiana* Mont. as being distinct species. In 1858 ([14], pl. 25) Harvey illustrated a cystocarpic specimen of *M. obtusata* and placed both *M. abscissa* (Turner) Hook. et Harvey, *M. billardieri* Mont. and *M. jaubertiana* in synonymy under *M. obtusata*. Hooker ([18], p. 242; [19], p. 688), however, regarded *M. jaubertiana* as distinct from *M. abscissa*.

J. Agardh [5] described two more species from Australia: *M. concinna* J. Ag. from the Bass Strait and *M. polydactylis* J. Ag. from New South Wales.

In 1932 Kylin transferred *Melanthalia* from the *Sphaerococcaceae* to the Gracilariaceae and recognized three species: *M. concinna* J. Ag., *M. polydactylis* J. Ag. and *M. abscissa* (Turner) Hook. et Harv. in addition to the type species. Kylin [25] did not accept the conspecificity of *M. jaubertiana* Mont. with *M. abscissa*, but viewed that *M. jaubertiana* may be associated with *M. obtusata* instead.

In his study on the Marine Flora of New Zealand, Chapman [6] regarded both *M. abscissa* (Turner) Hook. et Harv. and *M. jaubertiana* Mont. as varieties of *M. obtusata* (Labill.) J. Ag. and, accordingly, made the new combinations *Melanthalia obtusata* (Labill.) J. Ag. var. *abscissa* (Turner) Chapman ([6], p. 309) and *Melanthalia obtusata* (Labill.) J. Ag. var. *jaubertiana* (Mont.) Chapman 1979 (p. 311).

Biosystematic studies are needed to critically assess the species and varieties of *Melanthalia* from Australia, Tasmania and New Zealand.

The vegetative morphology of *Melanthalia* was previously studied by Jönsson [21] and its reproductive development by Papenfuss [28].

Materials and Methods

Specimens examined in this study were collected in the drift, The Bluff, Ninety Mile Beach, New Zealand, 2.ix.74, by M. H. Hommersand, and deposited at NCU. Additional material was collected by W. Nelson in Island Bay, Wellington, New Zealand, 13.ii.89 and 8.ix.89 in low intertidal pool beneath *Cystophora* (NCU). Transverse and longitudinal sections were hand-sectioned with a platinum-chrome double-edged razorblade. Material was stained with aceto-iron-haematoxylin-chloral hydrate [31] and mounted in 1:1 Hoyer's medium:water according to the procedure of Hommersand and Fredericq [16, 17].

Abbrevations

cp = carpogonium
f = fusion cell
ip = inner pericarp
hy = hypogynous cell
p = pericarp
su = supporting cell

Results

Vegetative organization

Thalli are up to 20 cm tall, consist of up to three orders of branches (Fig. 3), and are dark brown to almost black upon drying. Several terete to compressed axes depart from a basal attachment disc that, upon coalescence of several discs, resembles a rhizome-like holdfast. Each main axis has a subdichotomous to alternate branching pattern with prominent thickened apices.

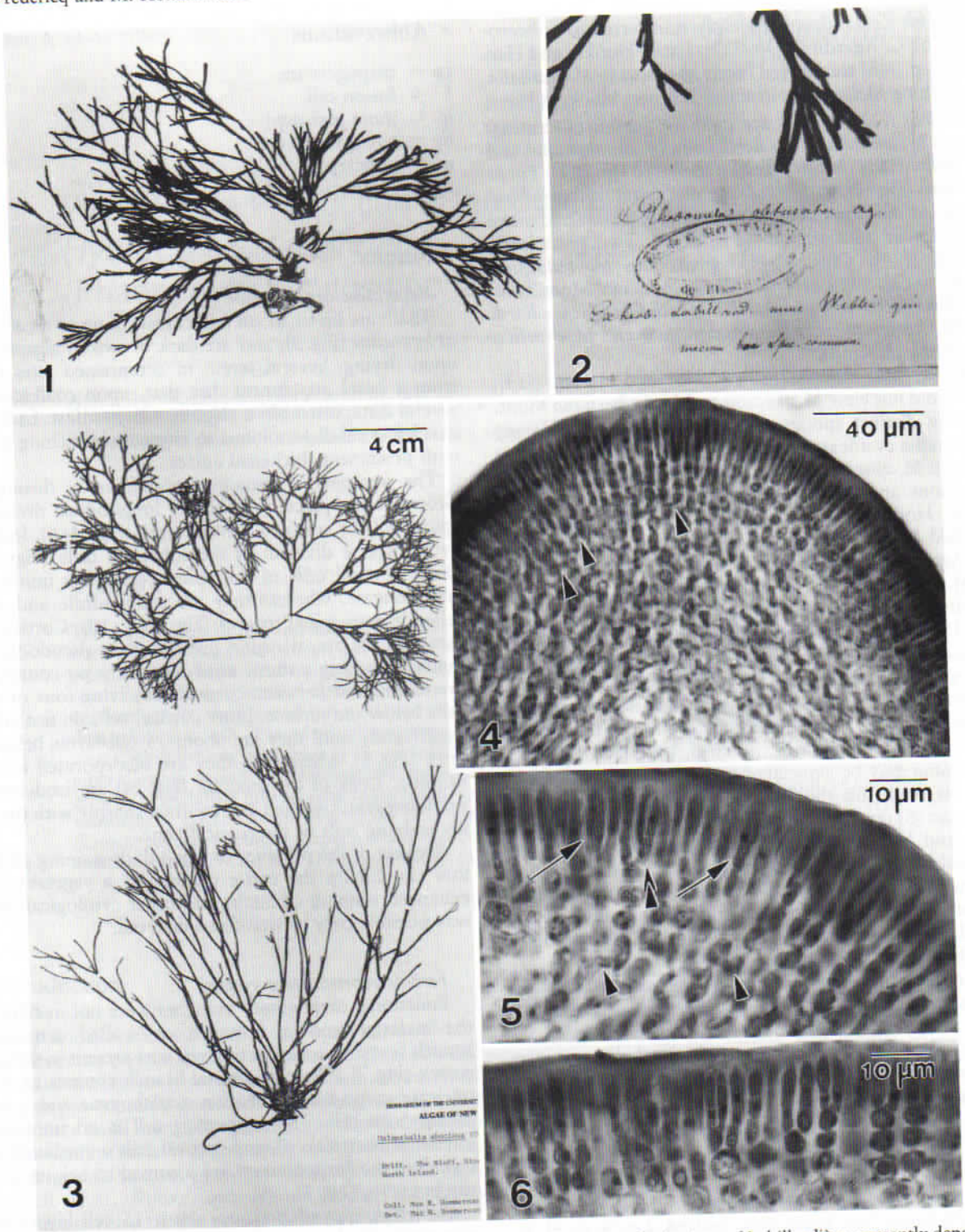
The anatomy is pseudoparenchymatous throughout. Growth takes place by obliquely longitudinal division of apical cells by concavo-convex septa (Figs. 4–6), followed by transverse division of the subapical cells (Figs. 5–6). Outer cortical cells of the apical region are uninucleate and elongate, whereas they are subquadrate and small-celled in non-apical regions (Figs. 7, 8, 10). Cortical filaments in the apical region preserve their pseudodichotomous branching pattern until secondary pit-connections are established between cortical cells lying four or more cells below the surface. Inner cortical cells do not enlarge significantly until they are about 15 cell layers below the apex (Fig. 5), whereupon they are incorporated into the medulla. Cells of the medulla (Fig. 14) are isodiametric, vacuolate, thick-walled and contrast sharply with the darkly staining cells ot the cortical zone.

Because of the presence of small dark-staining globules that can fill up the entire content of a vegetative cell, enhanced staining of nuclei and other cytological details was possible only in well-fixed material.

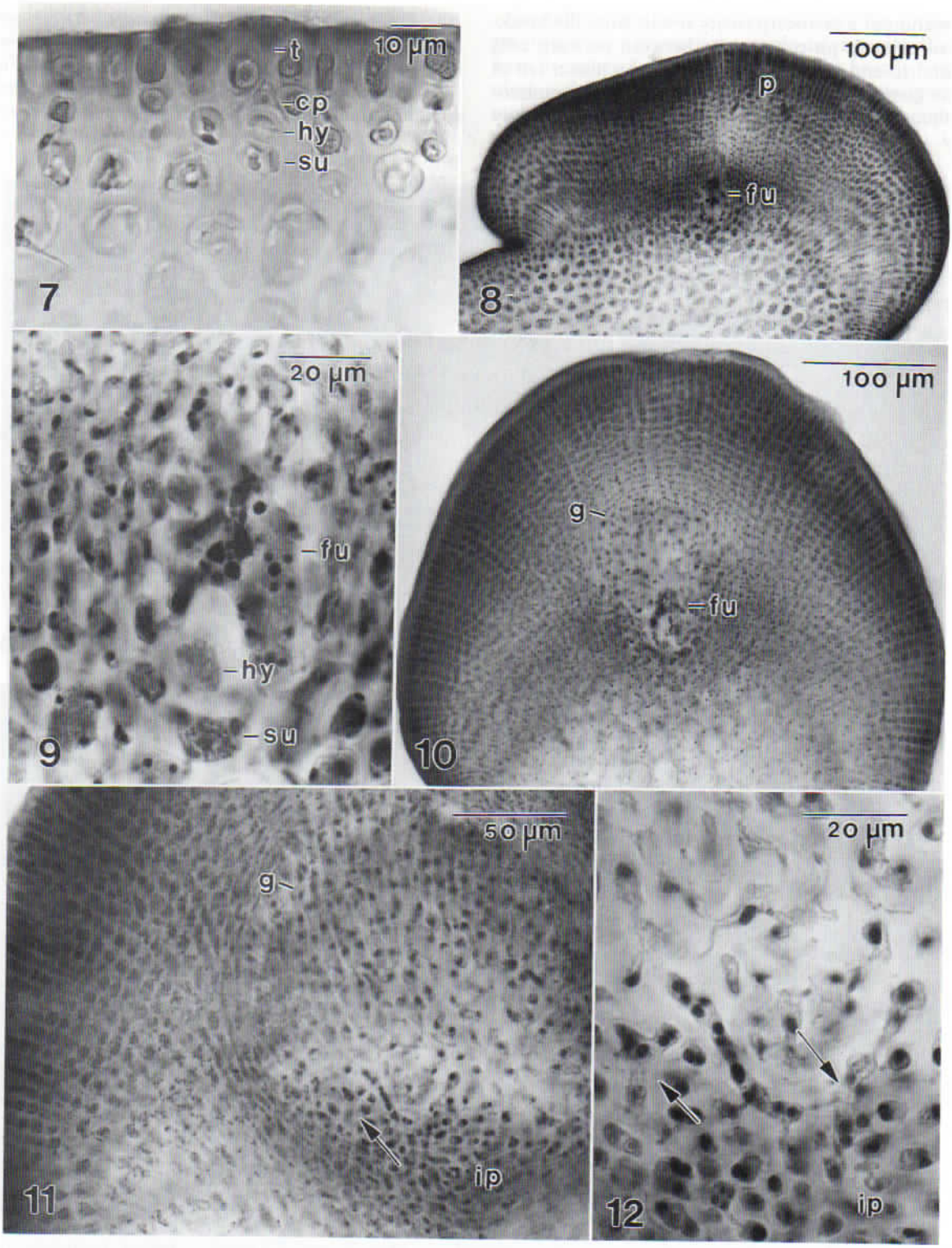
Female reproductive system

Functional carpogonial branches were not available in the material studied, however, a 2-called carpogonial branch borne on a supporting cell was present in the outer cortex (Fig. 7). The carpogonial branch consists of a uninucleate carpogonium bearing a trichogyne and a small hypogynous cell. The supporting cell is an unmodified intercalary cortical cell, and cortical cells immediately surrounding the carpogonium are assumed to belong to sterile branches (Fig. 7).

A well-developed pericarp about 15 cell layers thick surrounds the fusion cell completely by the time it has become multinucleate (Fig. 8). Pericarp cells typically remain small in size and their initial subquadrate shape is not modified by formation of secondary pit-connections. The fusion cell (Fig. 9) seems to originate in a typical Gracilariacean manner, with cells flanking the carponial branch fusing onto the carpogonium and bypassing the hypogynous cell which degenerates.



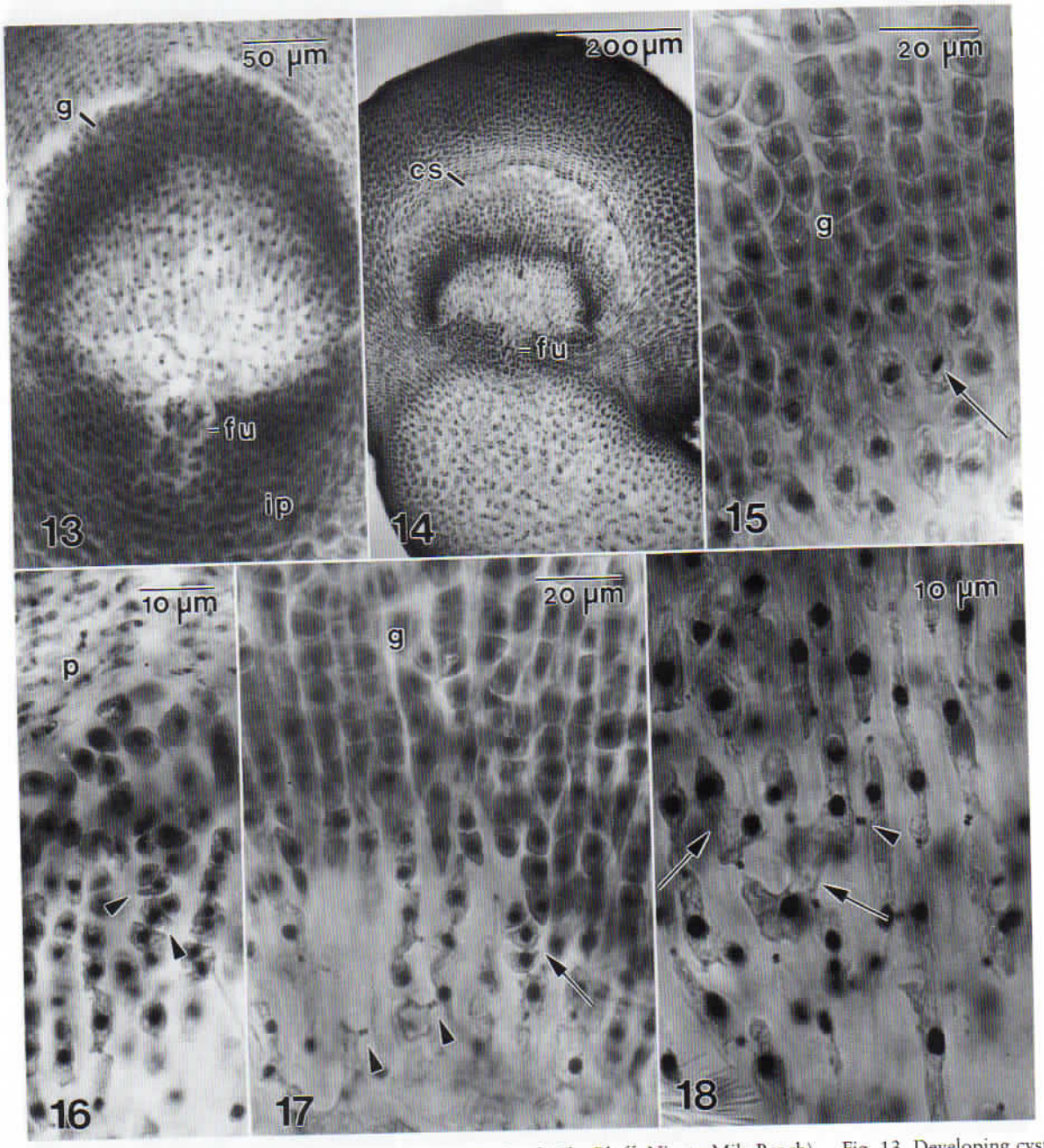
Figs. 1–2. *Melanthalia obtusata* – Fig. 1. Lectotype of cystocarpic specimen from the herbarium of Labillardière, presently deposited in the Montagne Herbarium, PC. – Fig. 2. Close-up of label belonging to specimen from Fig. 1. – Figs. 3–6. *Melanthalia obtusata* var. *abscissa* from New Zealand (The Bluff, Ninety Mile Beach). – Fig. 3. Habit of cystocarpic specimens. – Fig. 4. Longitudinal section of apex, showing outer cortical zone becoming incorporated into the medulla at level of formation of secondary pit-connections (arrowheads). – Fig. 5. Close-up of apex showing obliquely longitudinal divisions by concavo-convex septa (arrows) of terminal cells, followed by transverse division of subterminal cell (double arrowhead), and formation of conjunctor cells (arrowheads). – Fig. 6. Cortical region close to apex, showing regular files of pseudodichotomous filaments.



Figs. 7–12. *Melanthalia obtusata* var. *abscissa* from New Zealand (The Bluff, Ninety Mile Beach). – Fig. 7. Degenerating 2-celled carpogonial branch borne on supporting cell. – Fig. 8. Well-developed pericarp surrounding post-fertilization fusion cell prior to initiation of gonimoblast. – Fig. 9. Supporting cell bearing degenerating hypogynous cell and multinucleate fusion cell. – Fig. 10. Fusion cell bearing gonimoblasts. – Fig. 11. Developing cystocarp with uninucleate gonimoblast cells and small, darkly staining inner pericarp, with fusion (arrow) between both tissues. – Fig. 12. Close-up of Fig. 11. Lower gonimoblast cells have fused (arrow) with inner pericarp cells, and fusion product incorporating additional vegetative cells.

Formation of a cystocarp cavity results from the breakdown of primary pit-connections between pericarp cells just distal to and immediately flanking the fusion cell at the time gonimoblast initials are formed. Young gonimoblast filaments fill the entire space of the cystocarp cavity (Fig. 10), resulting in very close contact between gonimoblast and gametophytic tissues. An extensive cystocarp cavity never develops even in mature cystocarps (Fig. 14).

Gametophytic tissues in the floor of the cystocarp surrounding the fusion cell become highly modified as goni-



Figs. 13–18. *Melanthalia obtusata* var. *abscissa* from New Zealand (The Bluff, Ninety Mile Beach). – Fig. 13. Developing cystocarp showing chains of gonimoblast cells borne on sterile gonimoblast, fusion cell and inner pericarp cells. – Fig. 14. Mature cystocarp with small, roundish carposporangia. Note the sharp demarcation zone between pericarp and medulla. – Fig. 15. Oblique orientation of metaphase plate (arrow) in intercalary gonimoblast cell that will initiate a lateral filament upon division. – Fig. 16. Occasional irregular oblique divisions of gonimoblast cells (arrowheads). – Fig. 17. Inner gonimoblast cells linked to oneanother by secondary pit-connections with broadened pit plugs (arrowheads) and bearing young (arrow) and older chains of gonimoblast cells. – Fig. 18. Inner gonimoblast cells linked to oneanother by secondary pit-connections with broadened pit plugs, (arrowhead), around which they can fuse, forming multinucleate centers (arrows).

moblast development proceeds, with the formation of very small, darkly staining cells up to a depth of about 10 cell layers (Figs. 11, 13, 14). These compose the inner pericarp.

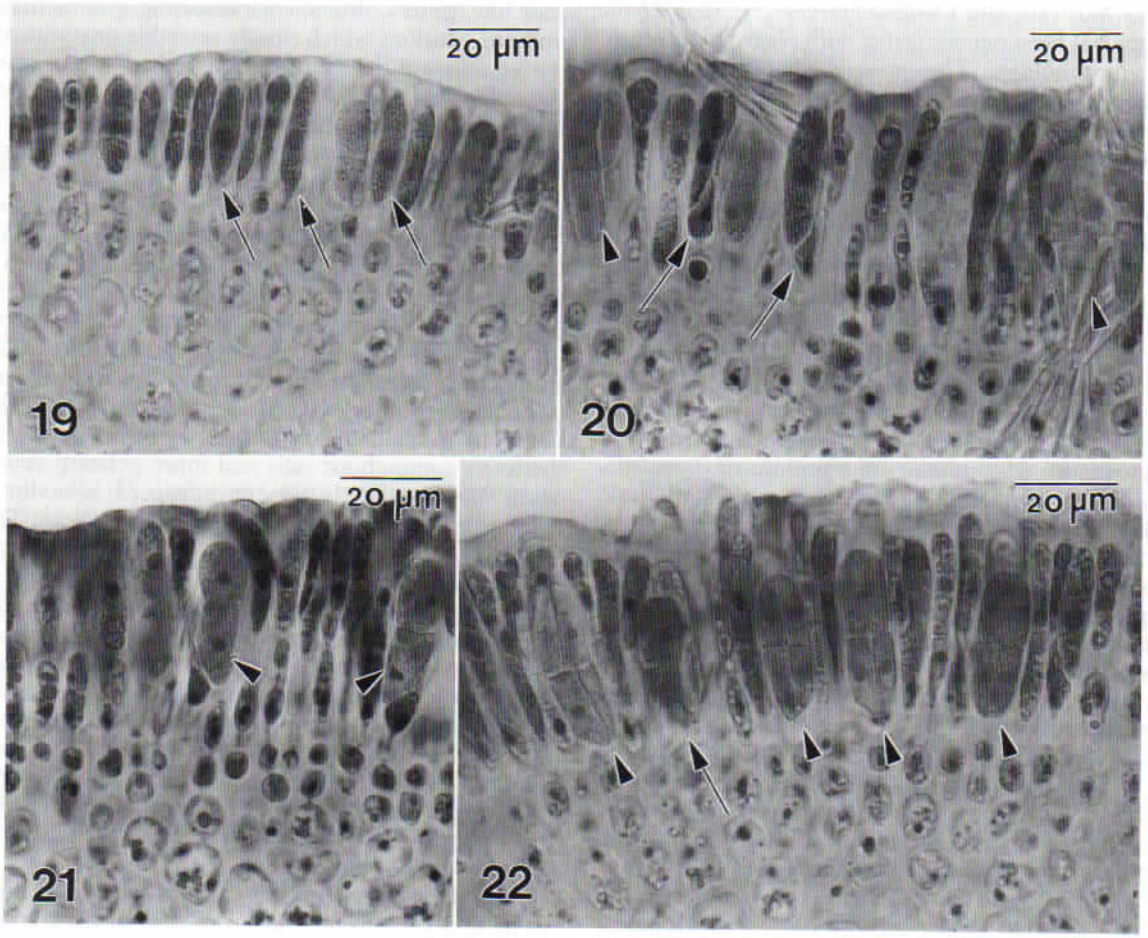
Gonimoblast cells are formed in rather straight chains due to transverse divisions (Fig. 15); however, occasional pronounced concavo-convex divisions give some gonimoblast filaments a zigzag shape. Initiation of a lateral filament is preceded by oblique orientation of the metaphase plate in an intercalary gonimoblast cell (Fig. 15), and branching is particularly common in zigzag-shaped gonimoblast filaments (Figs. 16, 17). Inner gonimoblast cells which have become vacuolate cut off conjunctor cells that form secondary pit-connections laterally between files of gonimoblast filaments. A sharp demarcation between the vacuolate sterile gonimoblast cells and the darkly staining cells of the inner pericarp is characteristic of *Melanthalia*. The innermost gonimoblast cells closest to the floor of the cystocarp fuse directly with cells of this nutritive tissue, resulting in multinucleate elongate or irregularly-shaped centers that can incorporate additional vegetative cells (Fig. 12, arrow on right).

In older stages, when carposporangia are formed, the pit-connections between the sterile inner gonimoblast cells have broadened pit plugs (Fig. 17). The broadening of pit plugs is followed by the local fusion of a few inner gonimoblast cells around the pit-connections which, upon dissolution, result in multinucleate centers (Fig. 18). Carposporangia are borne in long chains (Figs. 15, 17) which mature basipetally. A narrow ostiole through which the carposporangia are expelled originates late and arises through the breakdown of secondary pit-connections in the center of the pericarp.

Cystocarps are projecting, roundish, non-rostrate and occur most commonly on the distal parts of the pseudodichotomies, either singly or in aggregated clusters.

Tetrasporangia

Outer cortical cells that will produce the tetrasporangial initials elongate to about five times their normal length (Fig. 19), forming a local elevation. This raised cortical tissue, referred to as a 'nemathecium', can be seen with the naked eye as dark brown patches on both surfaces in the



Figs. 19–22. *Melanthalia obtusata* var. *abscissa* from New Zealand (The Bluff, Ninety Mile Beach). – Fig. 19. Elongate outer cortical cells (arrows) with enlarged nuclei that will issue tetrasporocytes. – Fig. 20. Tetrasporocytes basally pit-connected to laterally compressed bearing cells (arrows). – Fig. 21. Irregularly divided cruciate tetrasporangia (arrowheads) basally pit-connected to their bearing cells. – Fig. 22. Regularly divided cruciate tetrasporangia (arrowheads) and a bisporangium (arrow) embedded between elongate cortical cells.

distal parts of the thallus. Nuclei of the elongated outer cortical cells enlarge, upon which the cells divide by a concavo-convex septum. The apical derivative becomes the tetrasporangial initial (tetrasporocyte) and expands in width, while the bearing cell becomes laterally compressed (Figs. 20, 21). Division of the tetrasporocyte is successive resulting in regularly (Fig. 22) to irregularly (Fig. 22) cruciately divided tetrasporangia embedded between elongate vegetative cells. Secondary pit-connections are not formed in the nemathecium.

Spermatangia

Spermatangia were not seen and are unreported in *Melanthalia*.

Discussion

Along with the genera *Gracilaria* Greville [7], *Gracilariopsis* Dawson [8], *Gracilariophila* Wilson et Setchell *in* Wilson [11], *Hydropuntia* Montagne [as *Polycavernosa* Chang et Xia] [10] and *Curdiea* Harvey [9], *Melanthalia* Montagne has been reinvestigated with regard to its reproductive morphology. The present study corroborates Montagne's [27], J. Agardh's [4, 5] and Papenfuss' [28] placement of *Melanthalia* alongside *Gracilaria* Grev.

Seven genera are currently recognized within the Gracilariaceae [10]. All share a suite of key morphological characters: growth continuous through concavo-convex division of terminal cells followed by concavo-convex or transverse division of subterminal cells to produce a pseudoparenchymatous thallus; a supporting cell that bears a two-celled carpogonial branch flanked by sterile branches; a generative fusion cell that cuts off several gonimoblast initials; an ostiolate pericarp; schizogenous development of the cystocarp cavity; secondary fusions between gonimoblast derivatives and cells of gametophytic tissues.

Diagnostic for *Melanthalia* are a prominent dome-shaped apical zone consisting of parallel files of small, dark, cytoplam-rich, outer cortical cells of uniform size; globule-filled thick-walled vegetative cells; minimal space between the gonimoblast and pericarp (cystocarp cavity); an inner pericarp composed of small, darkly staining multinucleate cells; formation of small fusion centers in the floor of the cystocarp as result of terminal gonimoblast cells fusing directly onto inner pericarp cells, with the fusion products incorporating still additional cells; formation of fusion centers within the hyaline sterile gonimoblast due to fusion of laterally contiguous sterile gonimoblast cells; organization of upper gonimoblast cells into rather straight chains composed of small, round carposporangia; production of tetrasporangia in nemathecia.

Of the genera of the Gracilariaceae, the closest taxonomic affinities of *Melanthalia* are with *Curdiea*. Both genera form tetrasporangial nemathecia in the same way: patches of outer cortical cells elongate prior to cell division and a tetrasporangium is cut off terminally on an elongated, laterally compressed subapical cell flanking the tetrasporangium. In contrast to the other genera in the Gracilariaceae, cell division precedes enlargment and elongation of the outer cortical cell initiating the tetrasporocyte in both *Melanthalia* and *Curdiea*. This difference in tetrasporangial ontogeny is viewed here as the infrafamilial divergence point leading us to recognize two clusters of genera in the Gracilariaceae: 1) those in which the formation of secondary pit-connections is delayed in vegetative and tetrasporangial systems (*Curdiea, Melanthalia*), and 2) those that form aboundant secondary pit-connections continuously throughout the development of vegetative and tetrasporangial systems (*Gracilaria, Gracilariopsis, Gracilariophila* and *Hydropuntia*). We regard the first cluster which is restricted to the southern hemisphere as having retained the ancestral type of development, and consider it the more primitive one.

In the course of evolution, members of the Gracilariaceae (except for parasites) have scarcely diversified in their vegetative morphology while having undergone extensive changes in cystocarp morphology. Although nutrition of the carposporophyte is supported by extensive fusions in all genera, the exact nature of these fusions and the presence and character of any nutritive tissues present separate the genera. Members possessing gonimoblast cells initiating fusions which closely resemble unmodified vegetative cells are the more primitive. In *Gracilariopsis* and *Gracilariophila* gonimoblast conjunctor cells establish secondary pit-connections with cells in the floor of the cystocarp. In *Gracilaria* multinucleate tubular nutritive cells fuse either onto pericarp cells or cells in the floor of the cystocarp. In *Hydropuntia* they fuse only to cells of the inner pericarp in the floor of the cystocarp. In *Curdiea* and *Melanthalia* uninucleate gonimoblast cells fuse into multinucleate inner pericarp cells, followed by further fusions of such cells around existing pit-connections. Formation of gonimoblast conjunctor cells (*Gracilariopsis, Gracilariophila*) is considered more primitive than production of tubular nutritive cells (*Gracilaria, Hydropuntia*). The production of small fusion centers involving direct fusions between gonimoblast cells and inner pericarp cells (*Curdiea, Melanthalia*) is also an advanced behavior parallelling that seen in *Gracilaria* and *Hydropuntia*). The character of the inner pericarp varies in the different genera. In *Gracilariopsis*, it consists of a large-celled tissue containing enlarged nuclei. In *Hydropuntia* it is composed of several layers of small-celled tissue. An inner pericarp is lacking in *Gracilaria*, a situation considered specialized. The most extensive nutritive tissues are found in *Curdiea* and *Melanthalia* where they are composed of a small-celled, small-nucleate inner pericarp that is viewed as a nutrient processing center that persists and functions up to the final stages of cystocarp development. The absence of an inner pericarp in *Gracilariophila* is interpreted as a secondary loss due to parasitism.

Formation of the primary fusion cell is established in Gracilariaceae through fusion of cells of the sterile branches onto the carpogonium. Only a primary fusion cell is formed in *Melanthalia, Curdiea, Gracilariopsis* and *Gracilariophila*. A more advanced condition in which additional fusions with vegetative cells follow to form a ramified fusion cell (secondary fusion cell) occurs only in *Gracilaria*

and *Hydropuntia*. The formation of a secondary fusion cell is interpreted as a specialized strategy designed to supply a high level of nutriment prior to gonimoblast initiation leading to fine control in regulating further carposporophyte growth. Tubular nutritive cells are formed in *Hydropuntia* and *Gracilaria* sparsely or frequently and either early or late within the same species or in different species, presumably depending on the levels of nutriment available in the fusion cell.

Each of the genera we have examined is characterized by a distinct cystocarp morphology reflecting the type of nutritive tissue formed by the gametophyte and its interaction with the carposporophyte through secondary fusions. Our generic concept in the Gracilariaceae is based on the differentiation of these tissues and their interactions.

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Key words: Gracilariales, *Melanthalia*, morphology, taxonomy, Rhodophyta

Suzanne Fredericq, Department of Botany, National Museum of Natural History, Smithsonian Institution, Washington DC 20560, USA