Reproductive morphology and development of the cystocarp in *Curdiea flabellata* Chapman (Gracilariales, Rhodophyta)

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Abstract Based on features of the reproductive morphology in *Curdiea flabellata* from New Zealand, *Curdiea* is a distinct genus within the Gracilariaceae. Diagnostic are the complete absence of sterile gonimoblast tissue within the cystocarp; early cytological modification of the inner pericarp; an extensive network of secondary fusions between carposporophytic and gametophytic tissues in which gonimoblast cells fuse onto inner pericarp cells, followed by further fusions of cells in the floor of the cystocarp around existing pit-connections; fusion of gonimoblast cells directly with the fusion cell around primary pit-connections; organisation of all but the most basal gonimoblast cells into long chains; basipetal development of the small carposporangia; production of tetrasporangia in nemathecia.

The functional morphology of the nutritive tissue of cystocarps is briefly reviewed in other genera of the Gracilariaceae.

Keywords *Curdiea*; Gracilariaceae; morphology; reproduction; Rhodophyta; systematics

INTRODUCTION

The genus *Curdiea* was described by Harvey (1855:333) and typified with a new species from southern Australia, *C. laciniata*, based on cystocarpic and tetrasporic drift material. Diagnostic characters of *Curdiea* included possession of a flattened, coriaceous–membranaceous, laciniate, leafy, or often marginally pinnate, two-layered thallus; large, round-angular, medullary cells that gradually decreased in size towards the surface, and small cortical cells in anticlinal rows; fleshy, marginal, globose, sessile cystocarps; radiating gonimoblast filaments with small carposporangia; a thick ostiolate pericarp, and cruciately divided tetrasporangia within marginal nemathecia.

Harvey (1855) placed *Curdiea* in the "Sphaerococcoideae" next to the section *Podeum* of *Gracilaria*. *Podeum* included those species (J. Agardh 1852) with a flattened, distichously pinnate or dichotomous thallus, cystocarps on a flattened surface, and tetrasporangia embedded between short outer cortical filaments. Kylin (1930) did not initially include *Curdiea* in his new family Gracilariaceae, but did so in 1932. Additional taxonomic characters have not been reported for *Curdiea* since Harvey's original description. *Curdiea* continues to be maintained generically distinct from *Gracilaria* Greville by the possession of tetrasporangial nemathecia and carposporangia arranged in straight rows (Kylin 1932, 1956; Chapman 1979). Since Kylin (1932), the Gracilariaceae has been retained in the Gigartinales until recently when the family was transferred to the new order Gracilariales (Fredericq & Hommersand 1989a).

The aim of this study is to investigate the generic circumscription of *Curdiea* based on a morphological analysis of cystocarp development in *C. flabellata*, a species closely related to *C. laciniata*.

HISTORY OF *CURDIEA FLABELLATA*

Chapman (1979) provided a new name, *Curdiea flabellata*, for the New Zealand alga commonly

referred to as *Curdiea coriacea* (Hooker et Harvey) J. Agardh. The nomenclatural history of *C. coriacea* is especially confusing as identical names have been applied to two different taxa, *Sphaerococcus coriaceus* Sonder from Australia, and *S. coriaceus* (Hook. et Harv.) Kützing from New Zealand.

Rhodymenia? coriacea Hook. et Harv. (1845:545) collected by Lyall from the Bay of Islands, is the basionym of *S. coriaceus* (Hook. et Harv.) Kütz. (1849:784). Later, Harvey *in* Hooker (1855:243) transferred the species to *Gracilaria coriacea* (Hook. et Harv.) Harv., and J. Agardh (1876:401) made the combination *Curdiea coriacea* (Hook. et Harv.) J. Ag.

At the same time that he established *Sphaerococcus coriaceus* based on Hooker & Harvey's basionym, Kützing (1849:755) merged *S. coriaceus* Sonder (1846:192) into *Rhynchococcus* Kütz. as *Rhynchococcus coriaceus* (Sonder) Kütz. Later, in a confusing move Kützing also (1869:12, tab. 34) merged *S. coriaceus* (Hook. et Harv.) Kütz. into *Curdiea obtusata* (Sonder) Harv. (1862, pl. 210). *Curdiea obtusata* was based on *Chondrus obtusatus* Sonder (1845:56), later transferred to *Rhodymenia* as *Rhodymenia obtusata* (Sonder) Sonder (1846:191). J. Agardh (1876:429) based his new genus *Tylotus*, recently transferred by Kraft (1977) to the Dicranemaceae (Gigartinales), on *Chondrus obtusatus* Sonder.

In all likelihood, Kützing (1869) made an error and meant to merge S*phaerococcus obtusatus* (Sonder) Kütz. rather than *S. coriaceus* (Hook. et Harv.) Kütz. into *Curdiea obtusata*, because his description (Kützing, 1849:884) of *S. obtusatus* was placed a paragraph ahead of *S. coriaceus*. Kützing's concept of *S. coriaceus* was excluded from Kylin's circumscription of *Curdiea coriacea*.

J. Agardh (1896:95) retackled the nomenclatural riddle regarding *Curdiea coriacea*. He realised that several taxonomic entities were passing under the same name and took the following action: (1) he accepted the transfer by Harvey (1847:90) of *Sphaerococcus coriaceus* Sonder into *Thysanocladia coriacea* (Sonder) Harv., and also placed *Rhynchococcus coriaceus* (Sonder) Kütz. in synonymy under *Thysanocladia coriacea* (Sonder) Harv.; (2) he retained *Rhodymenia coriacea* Hook. et Harv. as the basionym for *Curdiea coriacea* (Hook. et Harv.) J. Ag.; (3) he based his new species *Curdiea kuetzingiana* from south Australia on Kützing's (1868:33 tab. 95) interpretation of *S. coriaceus* (Hook. et Harv.) Kütz. Kylin (1932:60) agreed that *C. kuetzingiana* and *S. coriaceus* from Australia were distinct from *C. coriacea* from New Zealand, but was unable to determine whether or not the two Australian entities were conspecific.

Chapman (1979, pl. 111) located a specimen from the original collection of *Rhodymenia? coriacea* Hook. et Harv. from Bay of Islands, New Zealand, in the Hooker Herbarium (BM), which did not conform to Kylin's (1932:61) concept of *Curdiea coriacea* as a coriaceous, laciniate taxon. Instead, it resembled an expanded form of *Curdiea crateriformis* (J. Ag.) Kylin (1932:61) [Basionym: *Sarcocladia? crateriformis* J. Ag., 1876:697, fig. 405]. Chapman therefore made the new combination *Curdiea coriacea* (Hook. et Harv.) Chapman for the taxon based on *Rhodymenia? coriacea* Hook. et Harv. and placed *Curdiea crateriformis* (J. Ag.) Kylin into synonymy under *C. coriacea*. Chapman (1979, pl. 111) interpreted the lectotype to be a specimen from the Bay of Islands collected by Hooker, *sd.*, whereas the original description states it was collected by Lyall. A second specimen from the same collection labelled "*Rhod.? coriacea*" dated September 1841 deposited in the Hooker Herbarium (BM) does not reveal the collector's name but may have been a Lyall collection, based on the handwriting. Hence, the more suitable lectotype of *Curdiea coriacea* (Hook. et Harv.) Chapman is the latter specimen.

Chapman (1979:304, pl. 112) provided a new name, *Curdiea flabellata* Chapman, for the species formerly interpreted as *C. coriacea*, and designated

Fig. 1–9 *Curdiea flabellata.*
Fig. 1 Cystocarpic specimen from Evening Cove, Paterson Inlet, Stewart Island, M. H. Hommersand, 5–6 December 1974. **Fig. 2** Transverse section through main branch. **Fig. 3** Initial of carpogonial branch system consisting of supporting cell and sterile branch initials (arrowheads). **Fig. 4** Degenerating 2–celled carpogonial branch borne on supporting cell bearing sterile cells (arrowheads). **Fig. 5** Sterile cells fusing (arrowheads) directly onto carpogonium, forming an incipient fusion cell. Fertilisation nucleus (arrow) inside boundary of original carpogonium. **Fig. 6** Same as in Fig. 5. **Fig. 7** Multinucleate fusion cell and darkly staining gametophytic cells (arrowheads). **Fig. 8** Multinucleate fusion cell and early formation of ostiole (arrowhead). **Fig. 9** Uninucleate (arrow) and binucleate (double arrow) gonimoblast initials cut off from fusion cell. (abbreviations: cp = carpogonium, hy = hypogynous cell, su = supporting cell, t = trichogyne.)
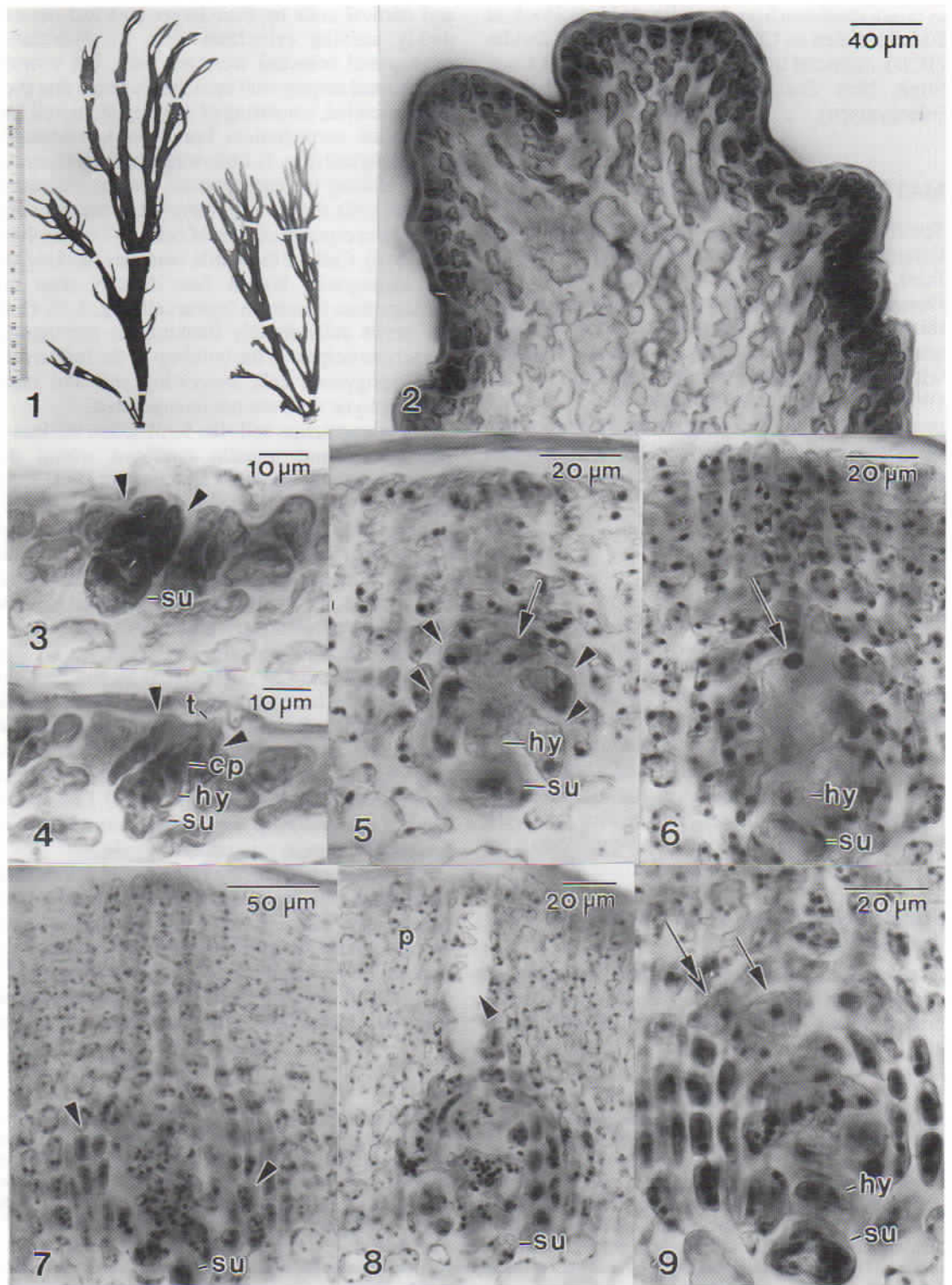
as type a specimen from Lyall Bay in Herb. Hook. at BM. Specimen no 132 from Trinity College, Dublin (TCD), collected in May 1849 by Lyall from Cook Strait, New Zealand, is designated as Isotype (=Isosyntype).

MATERIALS AND METHODS

Specimens examined include female and tetrasporangial plants from Evening Cove, Paterson Inlet, Stewart Island, collected by M. H. Hommersand, 5–6 December 1974. Material used in this study was fixed and preserved in 5% formalin/seawater. Transverse hand sections were stained with aceto-iron–haematoxylin–chloral hydrate (Wittmann 1965) and mounted in 1:1 Hoyer's mounting medium:water according to the procedure of Hommersand & Fredericq (1988). Herbarium abbreviations follow Holmgren et al. (1981).

RESULTS

Vegetative organisation

Thalli consist of one to several pink to purple brown, laciniate, flattened, coriaceous axes up to 20 cm tall arising from a single or coalesced holdfast (Fig. 1). Each axis tapers to a short, terete stipe, branches subdichotomously, often with bifurcated tips, and bears few to many marginal proliferations.

A transverse section through a main branch (Fig. 2) reveals a small-celled cortex consisting of predominantly transversely divided, subquadrate cells and a large-celled medulla. Secondary pit-connections are absent in the most distal cortical filaments.

Female reproductive system before and after fertilisation

At an early stage the female reproductive apparatus consists of a subcortical cell bearing two sterile branch initials. These differ from ordinary subcortical

and cortical cells by their larger size and denser, darkly staining cytoplasm (Fig. 3). Functional carpogonial branches were not seen, but aborted unfertilised carpogonial branches indicate that they are two-celled, consisting of a hypogynous cell and a terminal carpogonium borne on a subcortical supporting cell (Fig. 4). Following fertilisation, sterile cells flanking the carpogonium and neighbouring cortical cells divide transversely to form a young pericarp composed of files of cells 5–7 layers thick (Fig. 5, 6). Cells of the sterile branches flanking the the carpogonial branch fuse directly onto the carpogonium forming a fusion cell (Fig. 5, 6). Only the sterile cells directly flanking the carpogonial branch participate in the build-up of the fusion cell; the hypogynous cell, supporting cell and other gametophytic cells are not incorporated.

In young fusion cells the fertilisation nucleus is uninucleate and remains confined within the boundary of the original carpogonium (Fig. 5, 6). Later, the fusion cell becomes multinucleate (Fig. 7) prior to cutting off gonimoblast initials. At this stage the pericarp is 9–12 cell layers thick and an ostiole extends directly above the distal part of the fusion cell toward the thallus surface, formed by the breakdown of secondary pit-connections between centrally located pericarp cells (Fig. 7, 8). The hypogynous cell has degenerated by the time the fusion cell has become multinucleate. Gametophytic cells extending laterally up to four files of cells on either side of the fusion cell become modified cytologically and are darkly staining before gonimoblast initials are cut off (Fig. 7). Cells in the floor of the cystocarp that were produced prior to fertilisation remain unmodified.

A multinucleate fusion cell cuts off uninucleate initials from its upper end (Fig. 9). Nuclei within gonimoblast initials divide once or several times, and the gonimoblast initials enlarge, becoming bi- or multinucleate and irregular in shape (Fig. 9-12), occasionally sending out cytoplasmic protrusions (Fig. 10). Multinucleate gonimoblast initials next

Fig. 10–17 *Curdiea flabellata.*   ⇒

Fig. 10 Fusion cell with binucleate gonimoblast initial sending out lateral protrusion (arrow). Fig. 11 Another fusion cell with a binucleate gonimoblast initial (arrow). Fig. 12 Same as Fig. 11, but different focal plane. Multinucleate gonimoblast initial (arrow) has cut off two uninucleate gonimoblast cells (arrowheads). Fig. 13 Non-median section. Gonimoblast and darkly staining inner pericarp. Fig. 14 Broadened pit plugs (arrowheads) in region of fusion of gonimoblast cells with inner pericarp cells. Fig. 15 Gonimoblast cells have fused with inner pericarp cells (arrowheads) and with lateral gonimoblast cell around broadened pit plugs (arrow). Fig. 16 Fusion cell with gonimoblast, darkly staining inner pericarp and outer pericarp with ostiole (arrowhead). Fig. 17 Close-up of fusion cell in Fig. 16 at a different focal plane. Gonimoblast cells fused back to fusion cell around broadened pit plugs (arrowheads). (Abbreviations: f = fusion cell, g = gonimoblast, i = inner pericarp, su = supporting cell.)
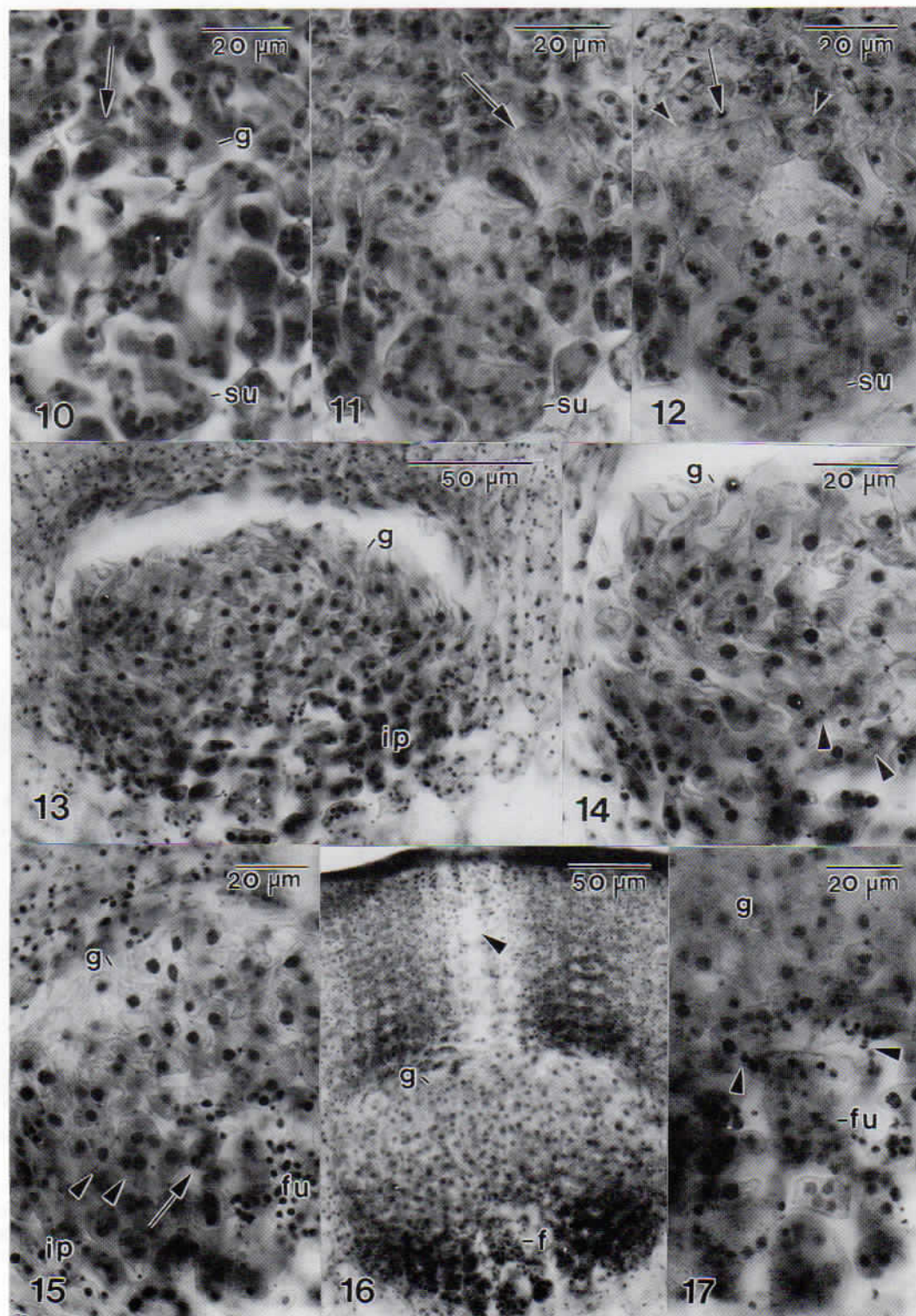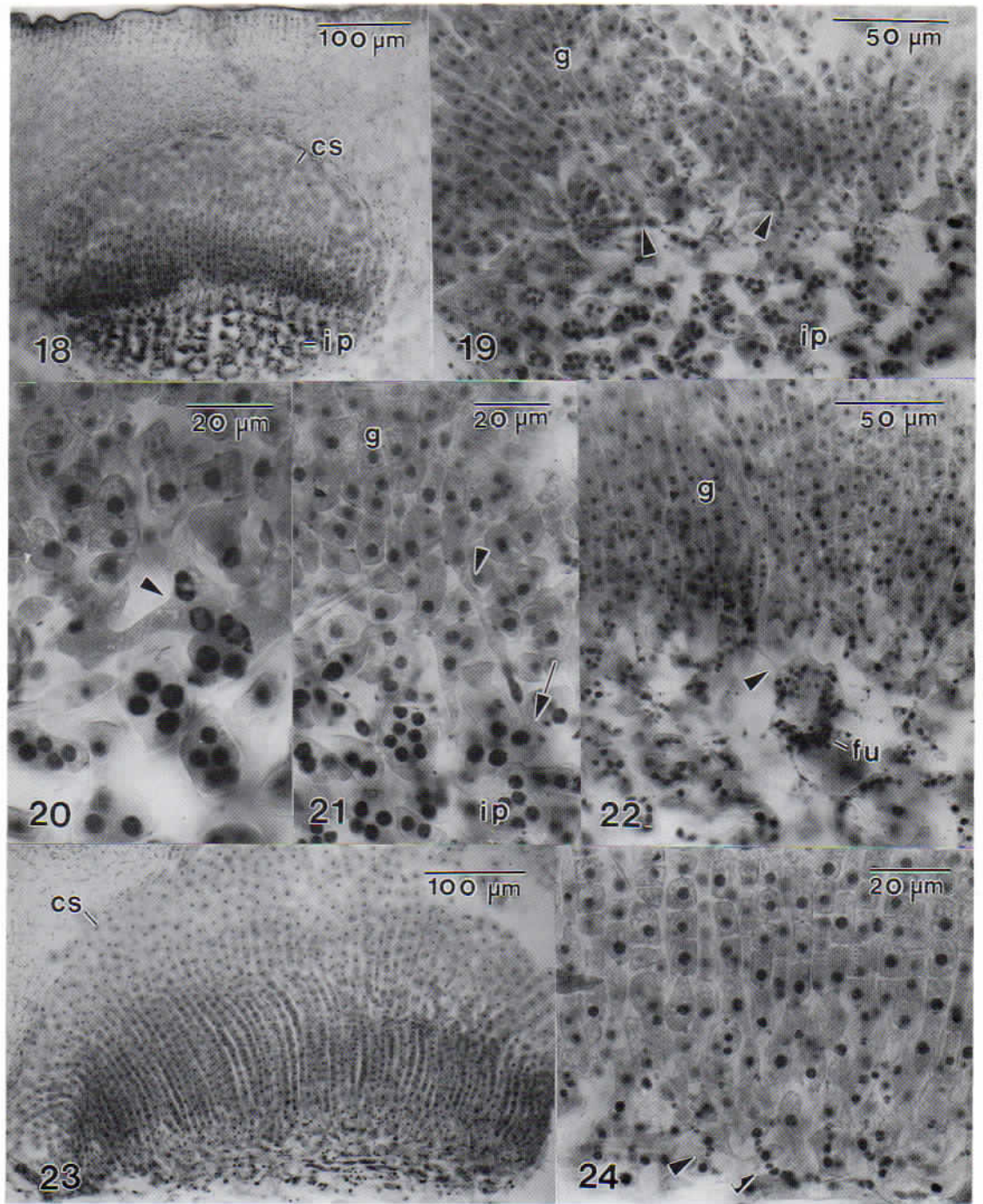
Fig. 18–24 *Curdiea flabellata.*
Fig. 18 Non–median section. Gonimoblast bearing carposporangia, and inner pericarp. Fig. 19 Fusion network (arrowheads) between gonimoblast cells and inner pericarp cells. Fig. 20 Fusion (arrowhead) between several inner gonimoblast cells and inner pericarp cells. Fig. 21 Intercalary gonimoblast cell forming a stretched process (arrowhead) that has fused with a floor cell (arrow). Fig. 22 Pit plugs connecting gonimoblast cells and fusion cell have dissolved (arrowhead). Fig. 23 Non-median section. Mature cystocarp with gonimoblast and maturing carposporangia in straight chains. Fig. 24 Fusion network consisting of inner gonimoblast cells and inner pericarp cells around broadened pit plugs (arrowheads). (Abbreviations: cs = carposporangium, fu = fusion cell, g = gonimoblast, i = inner pericarp.)
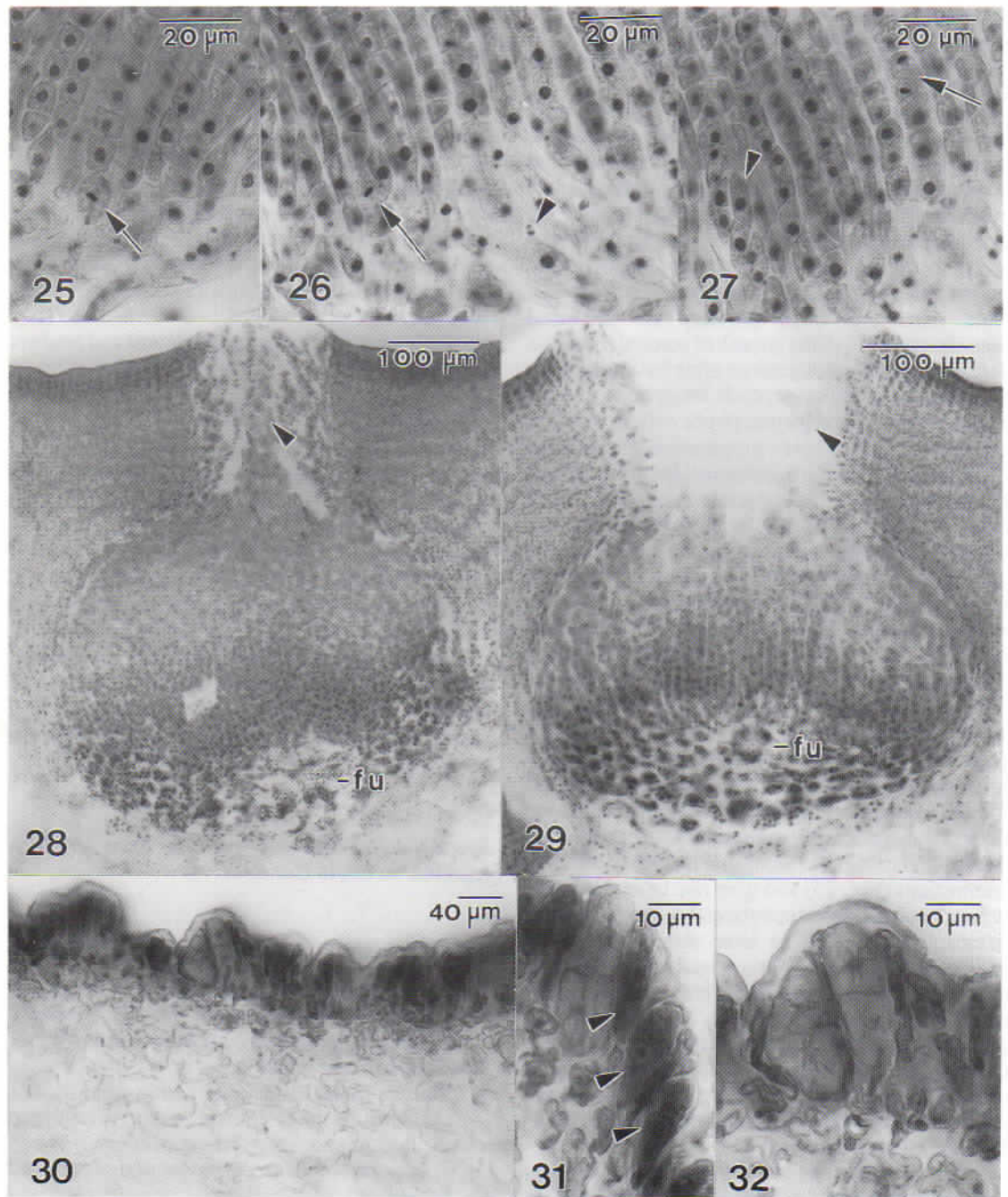
Fig. 25–32 *Curdiea flabellata*.
Fig. 25 Oblique position of metaphase plate (arrow) in inner gonimoblast cell. Fig. 26 Oblique position of metaphase plate (arrow) in intercalary gonimoblast cell bearing a lateral cell. Note broadened pit plugs (arrowhead) between inner gonimoblast cells and floor cells. Fig. 27 Oblique orientation of telophase (arrow) in intercalary gonimoblast cell that will initiate a lateral gonimoblast filament, similar to the one indicated by the arrowhead. Fig. 28 Mature cystocarp with ostiole (arrowhead) and released carpospores. Fig. 29 Same as in Fig. 28. Fig. 30 Nemathecial cortex. Fig. 31 Tetrasporocytes (arrowheads) subtended by narrow bearing cells. Fig. 32 Developing tetrasporangia and laterally compressed bearing cells.

cut off several uninucleate gonimoblast cells (Fig. 12), each of which continues to divide and forms gonimoblast filaments.

The cystocarp cavity is generated schizogenously through the breakdown of primary pit-connections between the distal files of pericarp cells and the cytologically modified gametophytic cells situated at the level of the fusion cell. Tissue distal to the cystocarp cavity forms the outer pericarp while the tissue in the floor of the cystocarp lateral to the fusion cell composes the inner pericarp (Fig. 13). Both inner and outer pericarp are produced secondarily through the growth of cortical filaments surrounding the carpogonium after fertilisation.

As the gonimoblast expands, the cystocarp cavity extends laterally and gametophytic cells in the floor of the cystocarp are progressively modified cytologically. Cellular transformations do not extend below the level of the supporting cell (Fig. 16) or beyond the base of the developing gonimoblast. The result is a sharply demarcated zone separating the gonimoblast, composed of uninucleate cells, and an inner pericarp, composed of multinucleate cells with enlarged nuclei (Fig. 13–16, 18). Cytologically modified, multinucleate inner pericarp cells are not incorporated into the fusion cell. Instead, uninucleate inner gonimoblast cells fuse directly with them (Fig. 14–15) without cutting off conjunctor cells. Pit plugs of cells in the vicinity of fusions typically broaden (Fig. 14). In addition, the fusion products formed from inner gonimoblast cells and cells in the floor of the cystocarp fuse laterally with one another. All fusions take place alongside the broadened pit-connections (Fig. 15) and give rise to an extensive network of fused gametophytic and carposporophytic tissues (Fig. 19–21). In later stages, intercalary gonimoblast cells may form stretched, uninucleate processes that fuse secondarily onto a cytologically modified inner pericarp cell (Fig. 21). The innermost gonimoblast cells connected to the fusion cell fuse directly with it (Fig. 17). Their pit-connections eventually disappear, leading to cytoplasmic continuity often with the formation of a candelabra-like central structure (Fig. 22).

An extensive zone of inner, sterile gonimoblast tissue is always absent. Gonimoblast cells not directly connected to the inner pericarp do not form secondary pit-connections with one another, and do not become vacuolate. As a result, gonimoblast filaments departing from the extensive fusion network formed from the lowermost gonimoblast cells and cells in the inner pericarp (Fig. 19–22) produce nearly straight chains that mature basipetally into carposporangia (Fig. 23, 24). Carposporangia remain small-celled and are nearly spherical upon release and expulsion through the ostiole (Fig. 28, 29).

A metaphase plate in a basal (Fig. 25) or intercalary (Fig. 26) gonimoblast cell, or an obliquely oriented telophase division figure (Fig. 27) will, upon completion of division, lead to the formation of a lateral gonimoblast filament. In this way, secondary gonimoblast filaments are added to the carposporophyte intrusively without disturbing the linear arrangement of older, maturing files of carposporangia.

Cystocarps are scattered over the thallus. They are partly sunk within the surface layers and tend not to project.

Tetrasporangia

When the cortical zone is activated to generate tetrasporangial initials in tetrasporophytic plants, patches of outer cortical cells elongate, forming locally raised cortical areas referred to as "nemathecia" (Fig. 30). An elongated outer cortical cell that is about to produce a tetrasporangium will divide by a concavo-convex septum into a terminal tetrasporocyte and a flanking subapical bearing cell. A tetrasporocyte stains darkly and has a prominent nucleus with a distinct nucleolus (Fig. 31), while the bearing cell is laterally compressed. Division of a tetrasporocyte is successive and typically gives rise to a cruciately divided tetrasporangium (Fig. 30–32).

Spermatangia

Spermatangia were not seen and have not been reported, so far, in *Curdiea*.

DISCUSSION

The present study confirms that, based on features of the reproductive morphology in *Curdiea flabellata*, *Curdiea* is a distinct genus within the Gracilariaceae. Diagnostic for the genus is:
(1) the complete absence of sterile gonimoblast tissue within the cystocarp, a property related to the lack of secondary pit-connections between gonimoblast cells or the production of enlarged vacuolated cells;
(2) early cytological modification of gametophytic cells produced after fertilisation (inner pericarp cells) lateral to the fusion cell in the floor of the cystocarp;
(3) formation of both outer and inner pericarps as a result of the schizogenous development of the cystocarp cavity through the breakdown of

secondary pit-connections across files of pericarp filaments above the level of the fusion cell;

(4) an extensive network of secondary fusions between carposporophytic and gametophytic tissues in which uninucleate gonimoblast cells fuse onto multinucleate inner pericarp cells, followed by further fusions of cells in the floor of the cystocarp around existing pit-connections;

(5) fusion of gonimoblast cells directly with the fusion cell around primary pit-connections;

(6) organisation of all but the most basal gonimoblast cells into long, straight, nearly parallell chains composed of small, cytoplasm-rich cells, most of which mature basipetally into small, round carposporangia;

(7) production of tetrasporangia in raised nemathecia in which each tetrasporangium is terminal on an elongated, compressed subapical cell flanking the tetrasporangium, much like a paraphysis.

Hommersand & Fredericq (1989) have documented that the functional morphology of the nutritive tissue of cystocarps is a useful tool for distinguishing between genera. Other Gracilariaceae, including the genera *Gracilaria* Grev., *Gracilariopsis* Dawson, *Gracilariophila* Wilson, *Hydropuntia* Montagne [including *Polycavernosa* Chang et Xia, see Wynne 1989], and *Melanthalia* Montagne, possess secondary pit-connections between gonimoblast cells and a large percentage of gonimoblast tissue by volume is sterile (Fredericq 1988). The floor of the cystocarp, which corresponds to an inner pericarp, is modified cytologically in *Gracilariopsis* (Fredericq & Hommersand 1989b), whereas in *Gracilaria* (Fredericq & Hommersand 1989a) and *Gracilariophila* (Fredericq et al. 1989) an inner pericarp is absent, and cytological transformations do not take place. The manner in which secondary fusions are established is also significant at the generic level. Gonimoblast cells establish secondary pit-connections with cells in the floor of the cystocarp by means of conjunctor cells in *Gracilariopsis* and *Gracilariophila*, whereas multinucleate tubular nutritive cells fuse either onto pericarp cells or cells in the floor of the cystocarp in *Gracilaria*, or only to cells of the inner pericarp in the floor of the cystocarp in *Hydropuntia* [as *Polycavernosa*] (Fredericq 1988). The absence of secondary pit-connections in the cystocarp of *Curdiea* appears to be compensated for by an increase in the diameter of pit plugs and, later, by fusions around pit plugs.

Curdiea shares some features of fusion cell formation and early stages of carposporophyte development with *Melanthalia* (Fredericq 1988). In both, patches of outer cortical cells elongate prior to cell division and a tetrasporangium is cut off terminally which is flanked by an extension of its bearing cell that is laterally compressed.

Approximately a dozen species of *Curdiea* have been described that are restricted to Australasia (e.g., Kylin 1932; Chapman 1979) and Antarctica (e.g., Lamb & Zimmerman 1977). Most were placed in *Curdiea* because they possess a flattened thallus and tetrasporangial nemathecia. The post-fertilisation features reported in this study will help to confirm their generic placement.

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