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Female Reproductive Morphology and Taxonomy of *Rhodopeltis* Harvey (Polyidaceae, Rhodophyta)

I. *R. australis* Harvey and *R. borealis* Yamada.

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Abstract

The female reproductive morphology of *Rhodopeltis australis* and *R. borealis* is described and illustrated. These two species fall well within the range of the Dumontiaceae with regard to the form of their carpogonial and auxiliary cell branches, connecting filaments, and carposporophyte development. They differ from typical species of this family mainly in their calcified thalli, superficial origin of carpogonial and auxiliary cell branches, and confinement of all female reproductive organs and carposporophytes to nemathecia. It is proposed that *R. australis* and *R. borealis* be transferred to the Dumontiaceae rather than maintained in the Polyidaceae (Gigartinales).

Key Words: morphology, taxonomy, *Rhodopeltis*, *Dumontiaceae*, *Polyidaceae*, *Gigartinales*, *Rhodophyceae*

The genus *Rhodopeltis* was established by Harvey (1863) on the basis of its nemathecia, which he misinterpreted as a parasite on a coralline alga, *Amphiroa australis* Sonder (1845). The "parasite" had previously been described by Harvey (1855) as *Cruoria australis*, from Western Australia. Schmitz (1889; in Schmitz & Hauptfleisch, 1897, p. 530) was the first to appreciate the fact that the "parasite" was the reproductive part of a thallus that had been incorrectly assigned to the Corallinaceae solely on the basis of its calcareous and articulated form. Weber-van Bosse (1904), apparently unaware of *Rhodopeltis*, reexamined a sterile frond of *Amphiroa australis* and decided that it represented a new genus of Corallinaceae, which she called *Litharthron*.

Four additional species have been assigned to *Rhodopeltis*, all from southern Japan and Taiwan: *R. borealis* Yamada (1931), *R. setchelliae* Yamada (1935), *R. gracilis* Yamada et Tanaka (in Yamada

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1935), and *R. liagoroides* Yamada (1935). The latter two species were placed in the genus with an expression of uncertainty.

Schmitz (1889, 1892) assigned *Rhodopeltis* to the family Rhizophyllidaceae, which included *Polyides*, *Ochtodes*, *Chondrococcus*, and *Contarinia* in addition to *Rhizophyllis*. Kylin (1956, p. 166) segregated *Polyides* and *Rhodopeltis* into their own family, which he named Polyidaceae (incorrectly spelled Polyideaceae). Schmitz assigned the Rhizophyllidaceae to the order Cryptonemiales, which he circumscribed to include all nonprocarpic Florideae with an indirect development of the carposporophyte, Kylin retained both the Rhizophyllidaceae and the Polyidaceae in the Cryptonemiales, although altering the ordinal definition to include Florideae with auxiliary cells borne on special accessory filaments or filament systems.

Harvey (1863) described and illustrated a cystocarpic nemathecium in *Rhodopeltis australis*, but details of the sexual reproductive system have remained unknown. In her monographic study of the genus, Nozawa (1963, 1970) observed only tetrasporangial thalli. Partly on the basis of Nozawa's observations on species of *Rhodopeltis* other than *R. australis*, Papenfuss (1966) transferred the Polyidaceae from the Cryptonemiales to the Gigartinales. However, the Cryptonemiales was included in Gigartinales by Kraft and Robins (1985).

Nozawa suggested that the five species of *Rhodopeltis* can be divided into two groups, with *R. australis* and *R. borealis* constituting the first group. Several morphological characters distinguish the two groups. The thallus is clearly segmented in the first group, while segmentation is inconspicuous in the second group. The growing point lies in an indentation of the terminal segment in the first group, while it lies at the pointed tip of the cylindrical branchlet in the second group. The cortical cells in the first group are round and occur in 7 to 9 layers, while those in the second group are elliptical and occur in 4 or 5 layers. Calcification begins in the outermost layer in the first group, while the outermost layer remains uncalcified in the second group. The medullary filaments are slender, much branched, and not very clearly connected with the cortical layer in the first group, while they are thicker, less branched, and clearly connected with the cortical layer in the second group. Tetrasporangia result from transverse divisions of terminal cortical or nemathecial cells in the first group, while they are borne on branched filaments below the surface of the thallus in the second group. All cells of the carposporophyte except those at the base become carposporangia in the first group, while only terminal cells of the dendroid gonimoblast become carposporangia in the second group. In addition, certain details of reproductive morphology that have not yet been studied in *R. australis* set *R. borealis* apart from the second group of species.

To clarify the generic definition of *Rhodopeltis* and its taxonomic position at the familial level, we have undertaken a study of the female reproductive structures of all five species. The present paper reports the results for *R. australis* and *R. borealis*.

Materials and Methods

Material of *R. australis*, comprising a few liquid-preserved segments with cystocarpic nemathecium, were provided by Peter Robins. These segments had been collected by Alan Millar at a depth of 15 m near Dyer Island, a small outcrop just off Rottnest Island, Western Australia, on December 4, 1984.

Cystocarpic plants of *R. borealis* were collected by the former author from Takarajima (July 11, 1978) and Kikaijima (May 26, 1979) in southern Japan, growing on a submarine terrace at low tide level to 3 m deep. Detailed studies of the female reproductive anatomy were made on liquid-preserved specimens. Sectioned materials were stained on the slide with aniline blue and then acidified with a drop of 1 N hydrochloric acid until enough stain had been absorbed. The sections were washed while on the slide and then mounted with corn syrup (Karo brand) preserved with thymol.

Observations

Rhodopeltis australis Harvey

The female reproductive organs and carposporophytes are immersed among nemathecial filaments (Figs. 8, 11, 16, nf). Observations on the few available specimens reveal that a nemathecium first appears on a subterminal segment and is well differentiated prior to the initiation of the female reproductive organs.

The carpogonial and auxiliary cell branches are initiated from superficial cells of the thallus and are spatially separated. It is difficult to distinguish one from the other in early stages of ontogeny (Fig. 1, fb), but, as they grow, they develop their own specialized forms. A carpogonial branch consists of six to eight cells, extending towards the outer surface of the nemathecium. The cells of a carpogonial branch are almost cylindrical while the carpogonium is hemispherical with a long terminal trichogyne (Figs. 2-8, tr). Cell division in the carpogonial branch is almost transverse in the lower part, whereas in the upper part it is oblique or sometimes almost longitudinal. Carpogonial branches are generally unbranched, but we observed one branch in which the subhypogynous cell bears a cell (Fig. 8, ru). In the young carpogonial branch, all cells stain in a similar manner, but subsequently their staining properties become differentiated. Commonly the third cell below the carpogonium stains more deeply with aniline blue than other cells of the branch. Because this cell often serves as the nutritive auxiliary cell, it seems reasonable to assume that there is a correlation between depth of staining and the nutritive function (Figs. 2-8, naux). The position of the auxiliary cell varies between three and five cells from the base of the branch, depending upon the length of the branch. The rudimentary cell on the subhypogynous cell (Fig. 8, ru) stains lightly.

In many carpogonial branches all cells have lost their staining capacity and have become modified in shape or size (Figs. 9 and 10). These carpogonial branches seem to be abortive.

Auxiliary cell branches are five (Fig. 12) to seven (Fig. 16) cells long, and the position of the auxiliary cell varies between three and five cells from the base of the branch. The auxiliary cell in the auxiliary cell branch is easily distinguished from the surrounding cells by its smaller size and, in contrast to the transverse divisions in other cells of the branch, by the characteristic oblique divisions between the cells just above and below it (Figs. 11 and 12, naux). The cells of the auxiliary cell branch are almost as long as broad, except the proximal ones, which are cylindrical.

Early post-fertilization changes in the carpogonial branch were not observed. Figs. 12 and 14 show carpogonial branches in which a stout primary connecting tube (pcon) from the carpogonium has established a union with the nutritive auxiliary cell (naux) in the carpogonial branch, which in turn has initiated several secondary connecting filaments (scon). The secondary connecting filaments are

septate and branch several times. During the development of these connecting filaments, the cells above the nutritive auxiliary cell (Fig. 15, naux) in the carpogonial branch disappear. A connecting filament fuses laterally with an auxiliary cell in an auxiliary cell branch (Figs. 16-20, naux), and generally goes on to make contact with additional auxiliary cells.

Fused segments of secondary connecting filaments cut off one or two gonimoblast initials, each of which produces a subdichotomously branched gonimolobe with almost all cells being transformed into carposporangia (Figs. 16-20, gl).

In contrast to those of *R. borealis*, the connecting filaments of this species are long-lasting and stain darkly with aniline blue. Thus, it is very easy to trace the connecting filaments for long distances in preparations of the squash method. Also, unlike *R. borealis*, gonimoblast initials are produced from their junction with the auxiliary cell (Figs. 14, 16, 18, 20-22, gl). In the latter case, the gonimoblast comprises a small number of full-sized carposporangia (Figs. 14, 21, gl). Auxiliary cells thus appear to have only a nutritive function.

The mature cystocarp forms a tightly clustered oblong mass of carposporangia, and the direction of gonimoblast development is outward (Figs. 16, 18, 20), lateral (Fig. 17), or even inward (Fig. 19).

***Rhodopeltis borealis* Yamada**

The female reproductive organs and carposporophyte are immersed among nemathecial filaments (Figs. 25, 28, 32). Nemathecia are uncalcified and are produced on the terminal one or two segments of the thallus. They are well differentiated prior to the initiation of the female reproductive organs.

The carpogonial and auxiliary cell branches are initiated from superficial cells of the thallus and are spatially separated. They are easily recognizable by the deep-staining properties and comparatively large size of their cells. In early stages of ontogeny, the two kinds of branches are similar (Figs. 23 and 24, fb).

When mature, a carpogonial branch consists of six to eight cells and is almost straight, extending towards the outer surface of the nemathecium. The cells of a carpogonial branch are almost cylindrical while the carpogonium is hemispherical with a long terminal trichogyne. A nutritive auxiliary cell (Fig. 26, naux) is present in each carpogonial branch and it is usually the subhypogynous cell, but its position varies between four and six cells from the base of the carpogonial branch, depending upon the length of the branch.

An auxiliary cell branch (Fig. 28) is seven to eleven cells long. The position of the base of the branch, suggesting that the auxiliary cells in the carpogonial and auxiliary cell branches are homologous. The auxiliary cells in both carpogonial (Fig. 26, naux) and auxiliary cell branches (Fig. 28, naux) are easily distinguished from the surrounding cells, even before fertilization, by their smaller size. The carpogonial and auxiliary cell branches are generally unbranched. In the only exception that I have observed, the subhypogynous cell bears a lateral branch that resembles the sterile terminal portion of an auxiliary cell branches (Fig. 29). Thus anomalous compound reproductive branch, along with the similarities in the ontogeny, staining properties, and auxiliary cell position in carpogonial and auxiliary cell branches, suggests that these branches are homologous structures in *Rhodopeltis borealis*.

Presumably after the receipt of a male nucleus, the carpogonium cuts off a small elongate cell

(Fig. 25, pcon) from its posterio-lateral face by a longitudinal division, and this cell establishes a connection with the nutritive auxiliary cell in the carpogonial branch. This connection is either by a direct fusion (Fig. 26) or by a secondary pit-connection (Fig. 32). It appears that the initial connection may occur by an open fusion with the connecting filament, which may subsequently form a pit connection.

The bridge thus made presumably facilitates the transfer of the diploid nucleus from the carpogonium to the nutritive auxiliary cell and is thought to be a primary connecting filament. After fusion with the nutritive auxiliary cell in the carpogonial branch, the primary connecting filaments may elongate directly (Fig. 26, pcon), or a new connecting filament may be initiated from the nutritive auxiliary cell (Fig. 32, scon). These secondary connecting filaments are septate, branch several times, and fuse laterally with auxiliary cells (Figs. 30-33, naux) in the auxiliary cell branches. Secondary connecting filaments generally go on to make contact with additional auxiliary cells. Except for those segments that have fused with auxiliary cells, the connecting filaments are ephemeral and only stain lightly.

The fused segments of a connecting filament cut off two to three gonimoblast initials (Fig. 30, gi), each of which produces a subdichotomously branched gonimolobe (Fig. 33) with almost all cells being transformed into carposporangia. The mature cystocarp forms a tightly clustered, oblong mass of carposporangia (Fig. 32, gl), or, occasionally, two lobes of carposporangia (Fig. 31, gl).

Figs. 34 and 35 show some unusual patterns of gonimoblast production. In Fig. 34, three gonimoblast initials have been produced from the primary connecting filament after its fusion with the auxiliary cell, which is located far below the carpogonium. Fig. 35 shows a cystocarp arising from a segment of connecting filament that has fused with the auxiliary cell in a carpogonial branch. In contrast to the situation illustrated in Fig. 34, there is no evidence of fertilization of the carpogonium or the subsequent production of a primary connecting filament. This situation suggests that if a carpogonial branch remains unfertilized it can function as an auxiliary cell branch, the auxiliary cell fusing with a connecting filament that originated from another carpogonial branch.

In all cases examined in this study, gonimoblast initials are produced from the connecting filament close to its junction with the auxiliary cell, and, although auxiliary cells are present in both carpogonial and auxiliary cell branches, both types only play a nutritive role in the development of gonimoblasts.

Discussion

From the present observations, *R. australis* and *R. borealis* are characterized by the following features: carpogonial and auxiliary cell branches produced from superficial cells, their ontogenies being similar and making it difficult to distinguish one from the other in early stages; initiation of carpogonial and auxiliary cell branches occurring late in the development of nemethecia; presumed fertilization of the carpogonium resulting in the formation of a primary connection with a nutritive auxiliary cell in the carpogonial branch and the subsequent production of secondary connecting filaments which extend towards the auxiliary cells in spatially distinct auxiliary cell branches; carposporogenous filaments arising from the connecting filament close or remote to its fusion with the

auxiliary cell either in the carpogonial or auxiliary cell branches; almost all cells of the gonimoblasts becoming carposporangia.

Some of these characters suggest that the assignment of *R. australis* and *R. borealis* to the Polyidaceae is untenable. In *Polyides lumbricalis* C. Agardh, the type and only species of its genus, the auxiliary cell is an undifferentiated cell of a vegetative filament (Thuret & Bornet, 1878; Kylin, 1923; Rao, 1956). In *Rhodopeltis australis* and *R. borealis*, by contrast, while both carpogonial and auxiliary cell branches are transferred nemathecial filaments, at maturity they are highly specialized. The two filaments have a similar ontogeny and the auxiliary cell in the auxiliary cell filament occupies a position comparable to that of the auxiliary cell in the carpogonial branch. Furthermore, gonimoblasts are produced from connecting filaments at a point close or remote to their union to auxiliary cells either in auxiliary cell filaments or in the carpogonial filament. It thus seems reasonable to conclude that carpogonial and auxiliary cell filaments are homologous in *Rhodopeltis* (as defined by its type species). Such a homology is also apparent in the fertilization development are similar to those in *Rhodopeltis*.

Many taxa of the Dumontiaceae have been carefully studied (e.g., Taylor, 1950, 1952; Lee, 1963; Abbott, 1968; Littler, 1974; Eiseman & Norris, 1981; Shepley & Womersley, 1983; Lindstrom, 1984; Millar & Kraft, 1984; Robins and Kraft, 1985). According to the results obtained by these authors, the Dumontiaceae appears to include some taxonomically diverse entities. Bert (1965) advocated the removal of multiaxial genera, such as *Dilsea* and *Neodilsea*, to the family Dilseaceae, although Abbott (1968) regarded the mutliaxial condition as scarcely sufficient for the establishment of a new family. The family Weeksiaceae was established for the three genera *Weeksia*, *Constantinea*, and *Leptocladia* because of unusual postfertilization events in which the carposporogenous filaments arise directly from a cell of the carpogonial branch (Abbott, 1968). A recent study of *Constantinea* by Lindstrom (1981), however, refutes the placement of this genus in the Weeksiaceae, indicating that it should be retained in the Dumontiaceae. *Rhodopeltis borealis* exhibits features in common with both the Dumontiaceae and the Weeksiaceae, i.e., the gonimoblast of this species are usually initiated from the connecting filament at a point close to its fusions with the auxiliary cells in the auxiliary cell branches, as in the Dumontiaceae, but occasionally from the connecting filament close to its fusion with the auxiliary cell in the carpogonial branch, suggesting a similarity with the Weeksiaceae. This intermediate situation suggests that separation of Weeksiaceae from Dumontiaceae is not feasible, and so, the Dumontiaceae may include taxa with functional and nonfunctional auxiliary cell branches, with uniaxial or multiaxial construction, and with or without nemathecia.

Although *R. australis* and *R. borealis* differ from the Dumontiaceae, notably in their calcified thalli and the superficial origin of their carpogonial and auxiliary cell branches, I believe that the similarities discussed above warrant the assignment of *Rhodopeltis* to that family. It should be noted that the removal of *Rhodopeltis* from the Polyidaceae.

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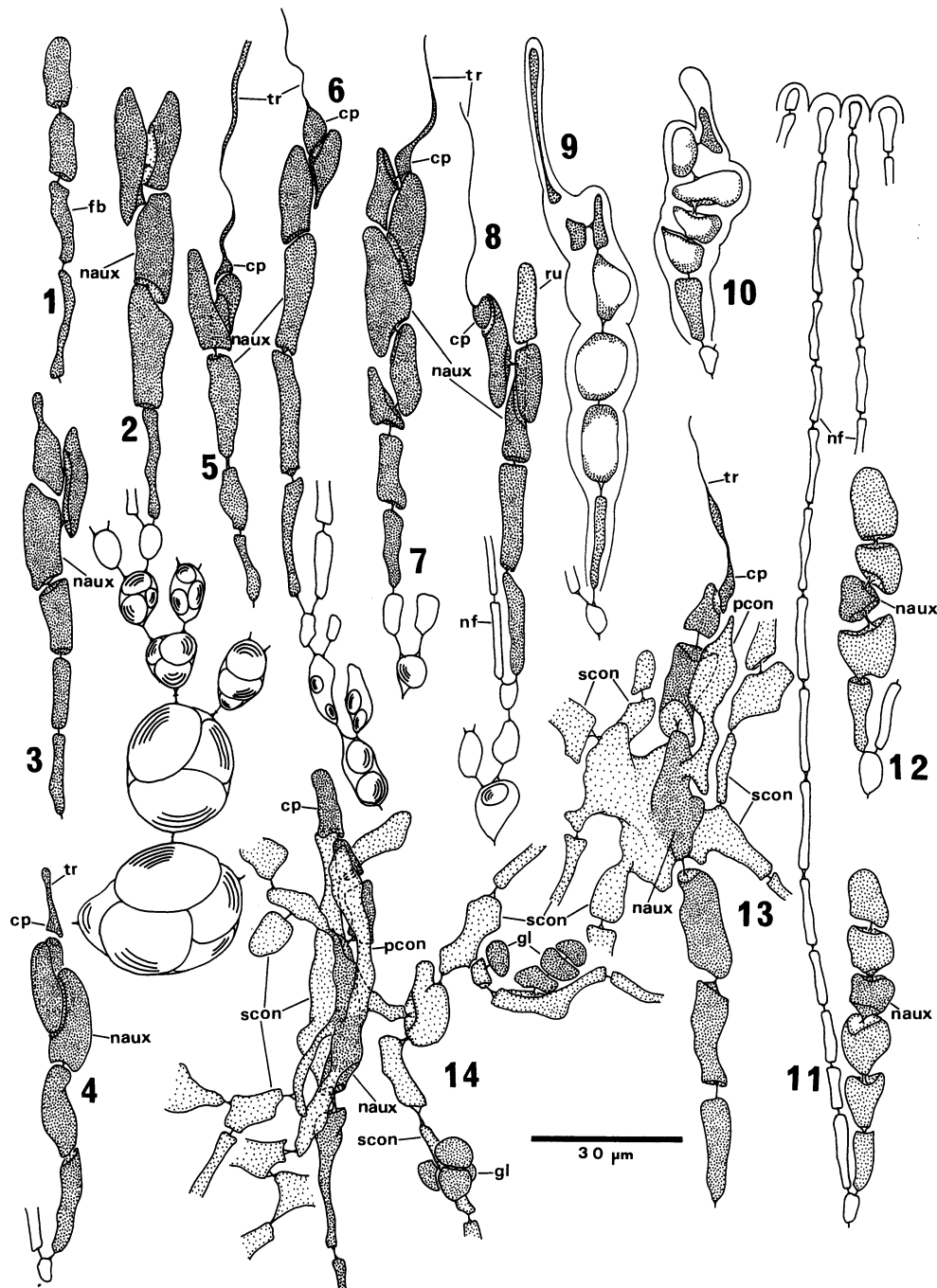
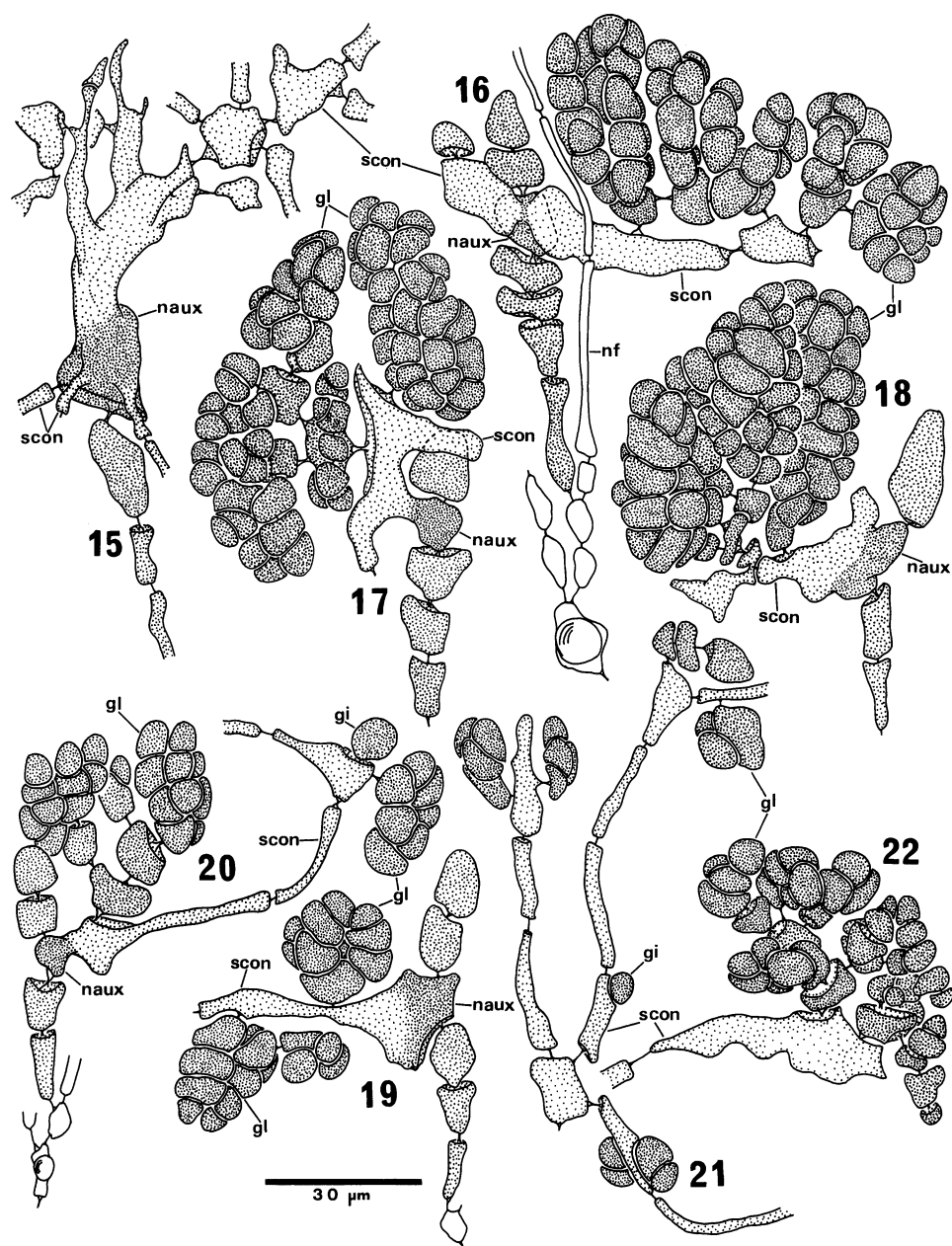
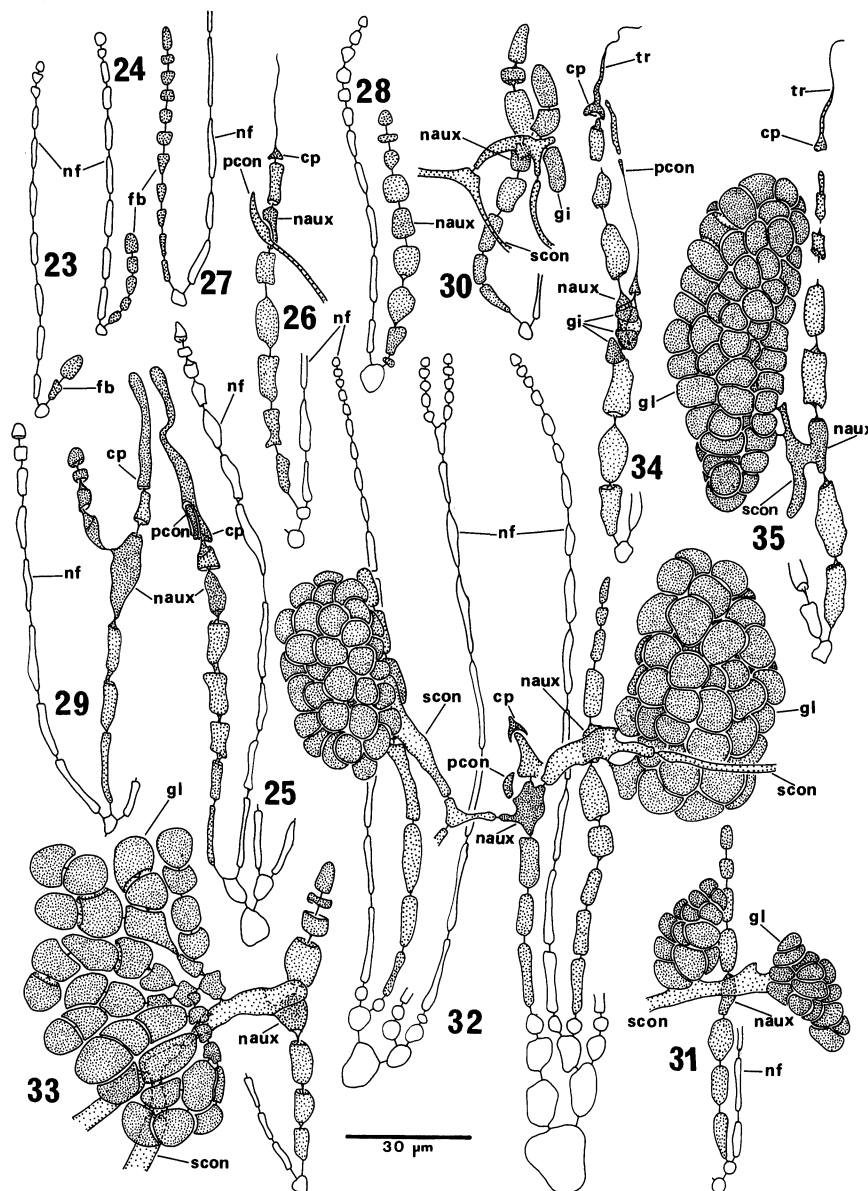
Figs. 1-14. *Rhodopeltis australis* Harvey

Fig. 1. Young fertile branch destined to become either a carpogonial or an auxiliary cell branch. Figs. 2-6. Development of carpogonial branch. Fig. 7. Carpogonial branch with cells cut off by conspicuous oblique divisions. Fig. 8. Carpogonial branch with rudimentary cell on subhypogynous cell. Figs. 9, 10. Abortive carpogonial branches. Figs. 11, 12. Auxiliary cell branches. Figs. 13, 14. Carpogonial branches with a primary connecting filament that has fused with a nutritive auxiliary cell and secondary connecting filaments emanating from a nutritive auxiliary cell in the carpogonial branch. In Fig. 14 some segments of the secondary connecting filaments have initiated gonimoblasts.



Figs. 15-22. *Rhodopeltis australis* Harvey

Fig. 15. Several secondary connecting filaments emanating from a nutritive auxiliary cell in the carpogonial branch. The cells of the carpogonial branch above the nutritive auxiliary cell have disappeared. Figs. 16-19. Mature cystocarps showing internal structure and direction of development on a secondary connecting filament. Figs. 20-22. Young cystocarps produced on segments of secondary connecting filaments at points remote from their fusion with auxiliary cells.



Figs. 23-35. *Rhodopeltis borealis* Yamada

Figs. 23-24. Nemathecial filaments with young fertile branch systems. Fig. 25. Carpogonial branch that has cut off a primary connecting filament. FIG. 26. Carpogonial branch with a primary connecting filament effecting union with a nutritive auxiliary cell in the carpogonial branch. Fig. 27. Young auxiliary cell branch. Fig. 28. Mature auxiliary cell branch. Fig. 29. Anomalous fertile branch which shares features of both carpogonial and auxiliary cell branches. Figs. 30-31. Auxiliary cell branch with young gonimoblasts borne on the connecting filament. Fig. 32. Carpogonial branch with secondary connecting filaments emanating from nutritive auxiliary cell and two auxiliary cell branches bearing mature cystocarps laterally on the connecting filaments. Fig. 33. Optical longitudinal section of mature cystocarp showing branching of the gonimoblasts. Fig. 34. Carpogonial branch with a primary connecting filament that has established a union with a nutritive auxiliary cell below. Fig. 35. Carpogonial branch functioning as auxiliary cell branch, with mature cystocarp borne at a point close to the nutritive auxiliary cell.

Abbreviations used of the Figures: cp=carpogonial branch; fb=branch destined to be fertile; gi=gonimoblast initial; gl=gonimolobe; naux=nutritive auxiliary cell; nf=nemathecial filament; pcon=primary connecting filament or tube; ru=rudimentary cell; scon=secondary connecting filament; tr=trichogyne.