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A new Order (Rhodogorgonales) and Family (Rhodogorgonaceae) of Red Algae Composed of Two Tropical Calciferous Genera, *Renouxia* gen. nov. and *Rhodogorgon*

Suzanne Fredericq[1,2] and James N. Norris[2]

[1] *Department of Botany, Duke University, Durham, North Carolina 27708–0338; and*
[2] *Department of Botany, NHB 166, National Museum of Natural History, Smithsonian Institution, Washington D.C. 205660.*

SUMMARY

A new red alga, *Renouxia antillana* gen et sp. nov., was found subtidally in Guadeloupe. *Renouxia* is characterized by flaccid, lubricous, lobed thalli which may bear blunt surface projections, giving a ruffled appearance; principal axes and defined meristem absent; thalli not differentiated into typical cortex or medulla but composed of loosely interwoven masses of indeterminate, pseudodichotomous assimilatory filaments bearing elongated, thin-walled rhizoidal filaments; apical cells dome-shaped, pigmented; sessile, scattered calciferous cells completely surrounded by calcite husks; 2-celled carpogonial branches; fertilized carpogonia initiating one to four diffusely branched gonimoblast filaments which ramify unilaterally among vegetative filaments; terminal cells of rhizoidal filaments growing towards and fusing with enlarged ends of intercalary gonimoblast cells, from which secondary gonimoblasts are initiated that produce terminal pairs of carposporangia. *Renouxia* shares with *Rhodogorgon*, another Caribbean alga, the following characters: calciferous cells with calcite husks; absence of defined meristem; uninucleate vegetative cells and absence of secondary pit connections; separate male and female gametophytes; subterminal clusters of spermatangial parent cells; absence of auxiliary cells and connecting filaments; and carposporangial development from diffusely branched gonimoblast filaments. *Renouxia* and *Rhodogorgon* are so significantly different from other red algae that they are placed in a new order (Rhodogorgonales) and new family (Rhodogorgonaceae) described herein.

Introduction

In the spring of 1990, specimens of an undescribed gelatinous red alga superficially resembling *Predaea* De Toni (Gymnophlaeaceae) [see e.g., 13] were collected at a depth of 10 m growing on hard corals of a patch reef situated among seagrass beds that separate the two islands of Guadeloupe, Grande Terre and Basse Terre (French West Indies). These algae, previously not observed in Guadeloupe, were abundant in the months following hurricane Hugo which passed over the islands on September 16–17, 1989 [1]. The plants are remarkable in their vegetative and reproductive anatomy, and represent a new genus, which, together with *Rhodogorgon* J. Norris et Bucher [18] constitute a new family and order.

Materials and Methods

Specimens investigated in this study were collected by SCUBA diving and fixed in the field in 5% buffered Formalin/seawater. Observations were made from microscope slides of small

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squashes prepared from liquid-preservered specimens. Preparations were either unstained, or briefly acidified on slides by 45% acetic acid to remove gelatinous substances, then stained with aceto-iron-haematoxylin-chloral hydrate [29] and mounted in 50:50 Hoyer's medium: distilled water according to the procedure of Hommersand and Fredericq [10], or mounted in 50% clear Karo: distilled water/1% aqueous aniline blue. Photographs were taken with a Zeiss Photomicroscope III using Kodak T-MAX 35 mm film. Type specimens, including liquid-preserved material, are deposited in the Algal Collection of the U.S. National Herbarium, National Museum of Natural History, Smithsonian Institution (US). Additional cited specimens are deposited in MEL, MICH, NCU, UC and US (herbarium abbreviations follow Holmgren et al. [9]). Spermatangial and carposporangial specimens of *Rhodogorgon carriebowensis* examined are deposited in US.

Results

Habit: Thalli are erect, flaccid, and very gelatinous, each consisting of several irregular lobes with broadly rounded margins which often bear whitish, blunt projections, giving the surfaces a ruffled appearance (Figs. 1–2). The pale-pinkish thalli are very slippery and come apart easily upon handling. They range from 2–5 cm in height and width and are centrally attached to the substratum by a short, dense stipe up to 3 mm long (Fig. 3) above a discoid holdfast. Thallus lobes may be superimposed (Figs. 1–2), or more openly spread (Figs. 3–4).

Vegetative development: Surface views (Fig. 5) and unstained squashes from a small piece of any thallus lobe reveal an abundance of brown, sessile, husk-like structures composed of calcium carbonate that are scattered singly and laterally on uniseriate assimilatory filaments below the uppermost five to six orders of branches (Figs. 6–8). The occurrence of the husk-like structures varies from abundant (Figs. 5–7) to rare (Fig. 11). They are always rare in portions of the stipe and holdfast where uniseriate filaments are less frequently branched. The husks are 12–15 μm broad, 25–30 μm long, and completely surround cells of the same length. When acetic acid or Wittmann's hematoxylin stain [29] is added to a specimen preparation, these husks dissolve immediately. We refer to the cells bearing the calcium carbonate as calciferous cells. These calciferous cells are initially unicellular, uninucleate, thin-walled, and hair-like with bulbous, hyaline bases (Fig. 9) and narrow channels terminated by blunt apices (Fig. 7) or inflated protoplasmic tips (Fig. 8). They frequently loose their cell contents (Figs. 7, 8) and the nuclei degenerate.

Protoplasm-rich calciferous cells may divide apically by transverse septa (Fig. 8) and continue to grow, extending into multicellular rhizoidal filaments (Fig. 10). By the time they have reached 40 μm in length, the husk-like coatings have disappeared. Rhizoidal filaments are typically thin-walled with darkly staining tips (Fig. 10). They may extend over long distances and intertwine among assimilatory filaments (Fig. 11). Rhizoidal filaments are about half the diameter of assimilatory filaments (2.5–3 μm vs. 5–8 μm).

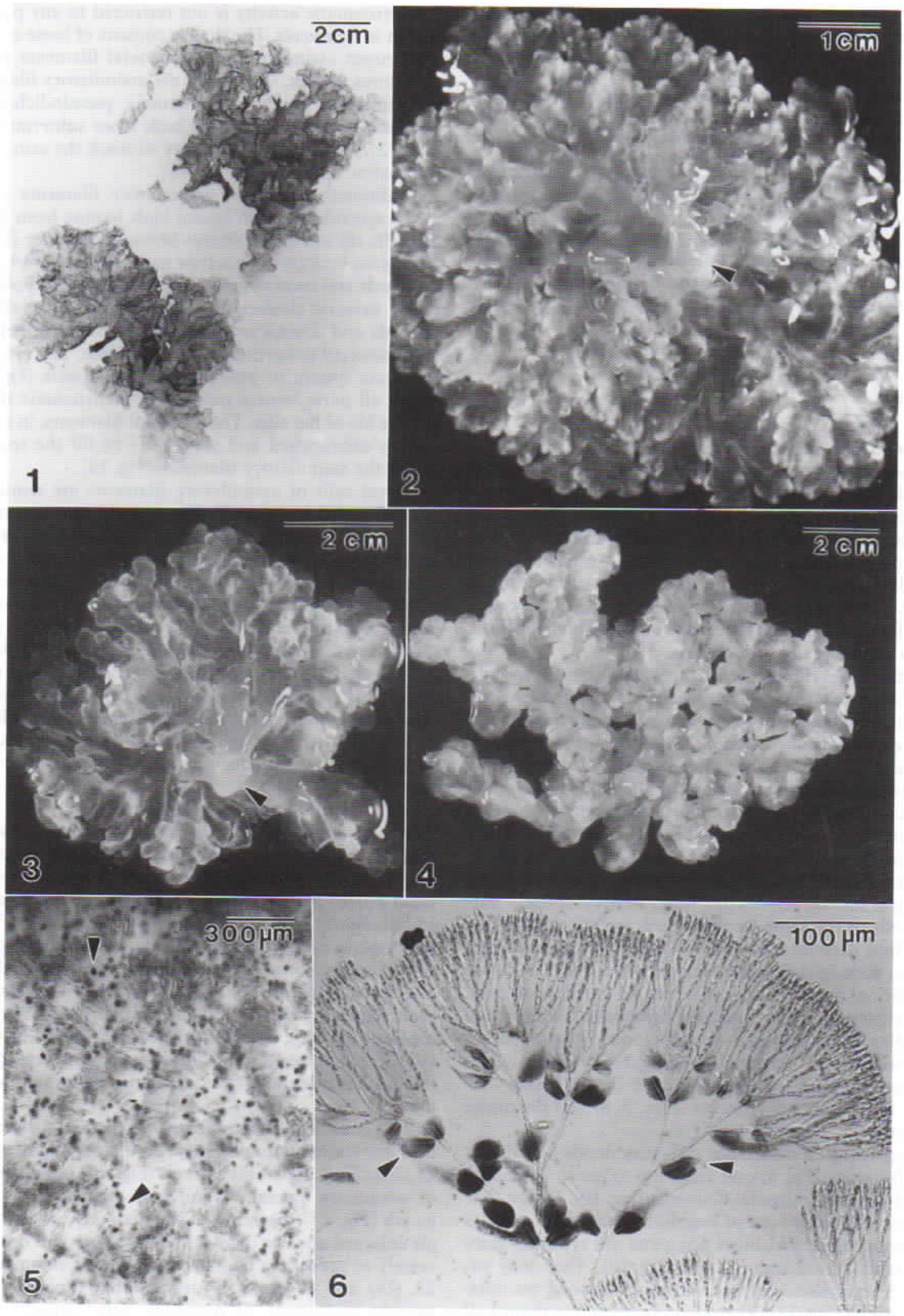
Meristematic activity is not restricted to any particular region in *Renouxia*. The thallus consists of loose masses of interwoven assimilatory and rhizoidal filaments within a gelatinous matrix. Growth of the assimilatory filaments is indeterminate and predominantely pseudodichotomous with the laterals initiated as buds from subterminal cells (Fig. 12). Assimilatory filaments all reach the same level at the thallus surface (Figs. 12–15).

Additional clusters of assimilatory filaments are produced secondarily from lateral buds issuing from intercalary cells six to eight segments below the surface (Figs. 13, 14). Most laterals of this type grow (Figs. 13, 14, arrow) outwards and form assimilatory filaments interpolated between existing clusters of filaments. Some initially grow inwards and downwards (Fig. 14, arrowhead) before being redirected towards the thallus surface. The result is an elaborate system of interconnected filaments (Fig. 15) in which all parts remain potentially meristematic throughout the life of the alga. The rhizoidal filaments, in contrast, remain unbranched and serve only to fill the spaces between the assimilatory filaments (Fig. 15).

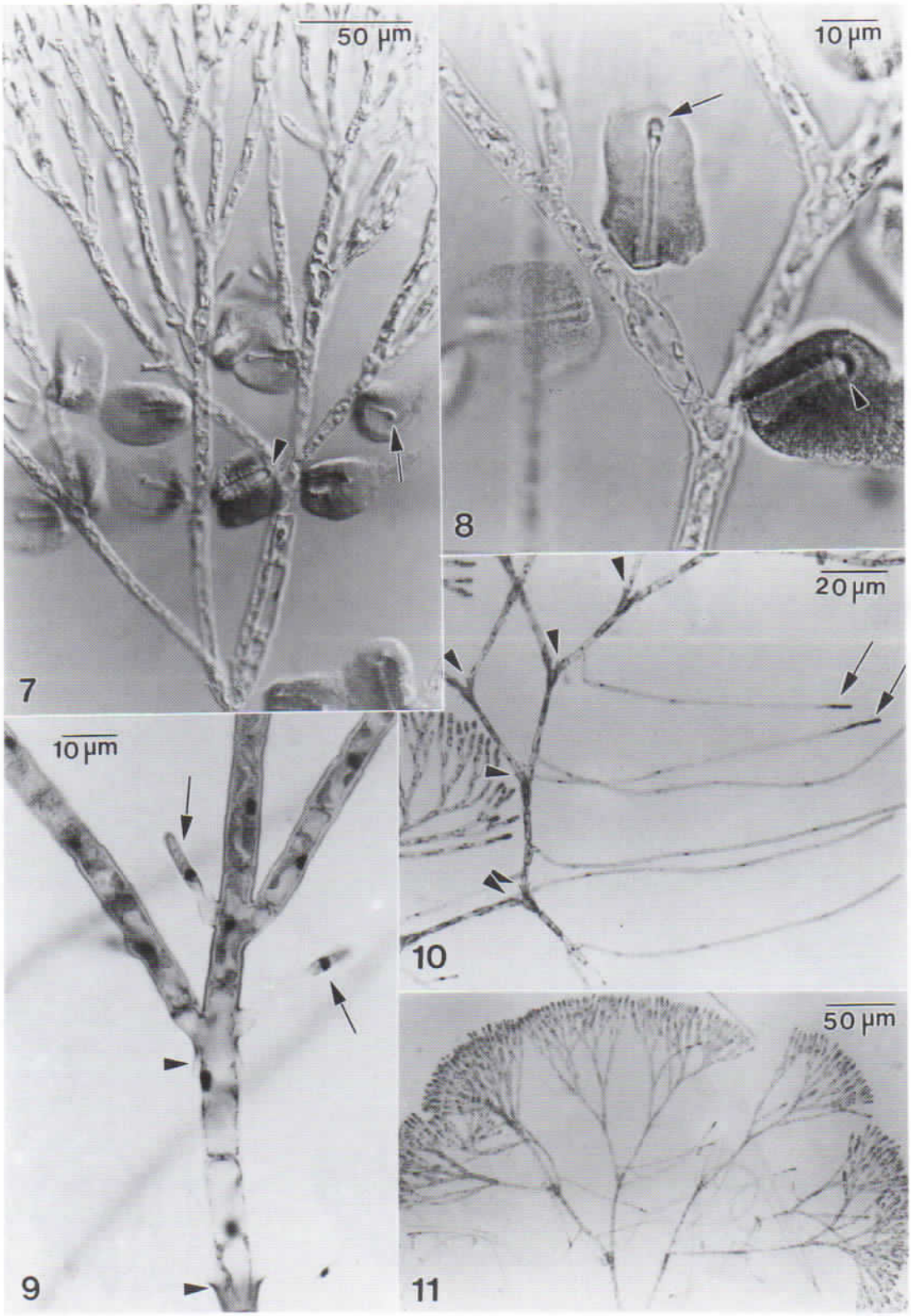
Apical cells of assimilatory filaments are densely pigmented and dome-shaped (Figs. 12, 13), measuring 5–20 μm long, 5 μm wide. Intercalary vegetative cells range in length from 15 to 25 μm and contain peripheral ribbon-shaped plastids (Fig. 9) which may break up into discoid plastids. Intercalary cells of assimilatory filaments elongate secondarily eight to ten segments below the surface, just below the points of initiation of secondary filaments. A characteristic feature of such intercalary cells is the persistence of ruptured outer cell walls that partly cover the thinner inner walls of the elongated intercalary cells (Figs. 9, 10). All vegetative cells are uninucleate and secondary pit connections or cell fusions between contiguous cells are absent.

Male reproductive development: Male and female structures occur on separate thalli. Spermatangia are produced in small subterminal clusters (Fig. 16). A subterminal cell of an assimilatory filament forms up to twelve small bulges (Fig. 17), each of which undergoes septation and elongates into a spermatangial parent cell (Fig. 18). Each spermatangial parent cells cuts off one (Fig. 19) to several spermatangia in succession by an oblique division. The spermatangial walls remain once the spermatia have been released (Figs. 20, 21). Assimilatory filaments may continue growing apically beyond the clusters of spermatangial parent cells (Fig. 20). Calciferous cells produce rhizoidal filaments less frequently in male than in female thalli.

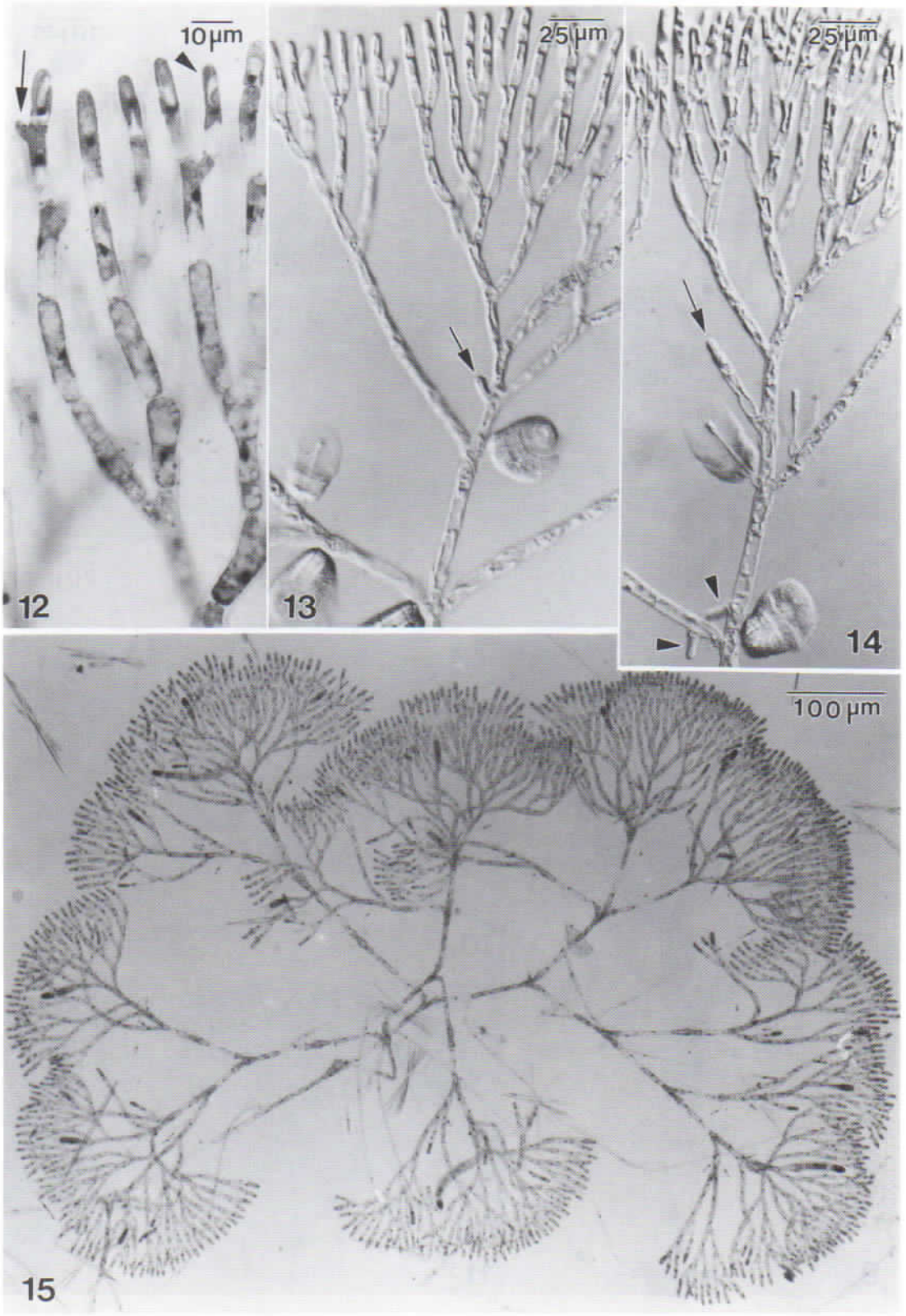
Prefertilization development: Carpogonial branch initials are scattered among the assimilatory filaments (Figs. 15, 22). They are sessile laterals (Fig. 23) or terminal cells of secondary lateral assimilatory filaments of varying length (Fig. 24). Each initial stains darkly, contains a single enlarged nucleus (Figs. 23, 24), and divides once transversely to produce a hypogynous cell that elongates (Figs. 23, 25) and a terminal carpogonium (Fig. 22) with a straight trichogyne. Hypogynous cells typically contain single, enlarged, darkly staining nuclei and are rich in cytoplasm (Figs. 23, 25).



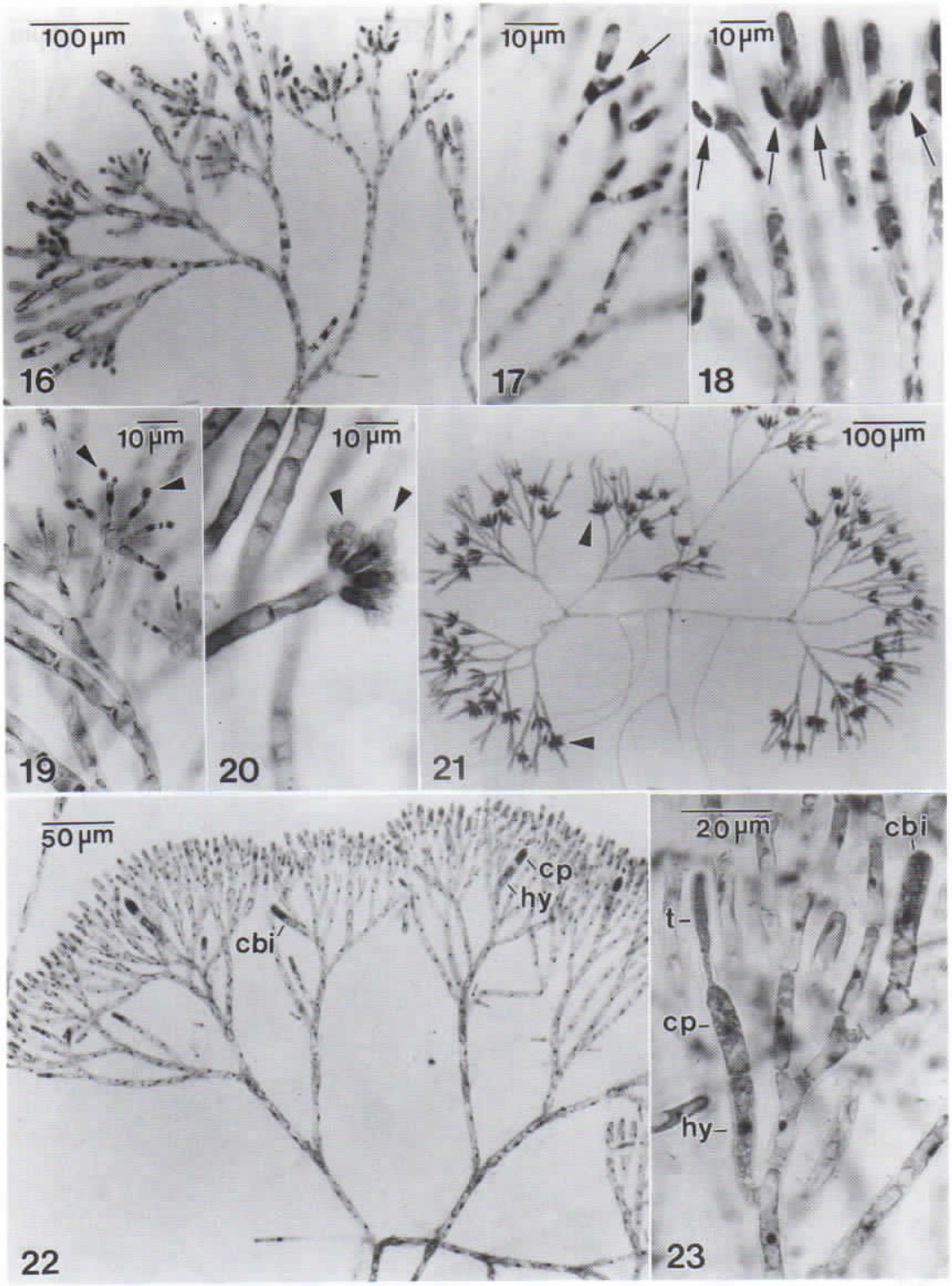
Figs. 1–4. *Renouxia antillana*, habits. – Fig. 1, Holotype, spermatangial plant (#*US-157157*); – Fig. 2, Isotype, spermatangial plant (#*US-157490*); – Fig. 3, Isotype, sterile plant (#*US-157491*); – Fig. 4, Paratype, carposporangial plant (#*US-157493*). Figs. 5–6. Unstained preparations of vegetative morphology; – Fig. 5, Surface view of part of lobe of the specimen in fig. 4 showing calcium carbonate (calcite) husks (arrowheads) and assimilatory filaments (#*US-157493*); – Fig. 6, Squash showing calcite husks (arrowheads) surrounding calciferous cells which are inserted laterally on assimilatory filaments below uppermost five to six orders of branches (#*US-157491*).



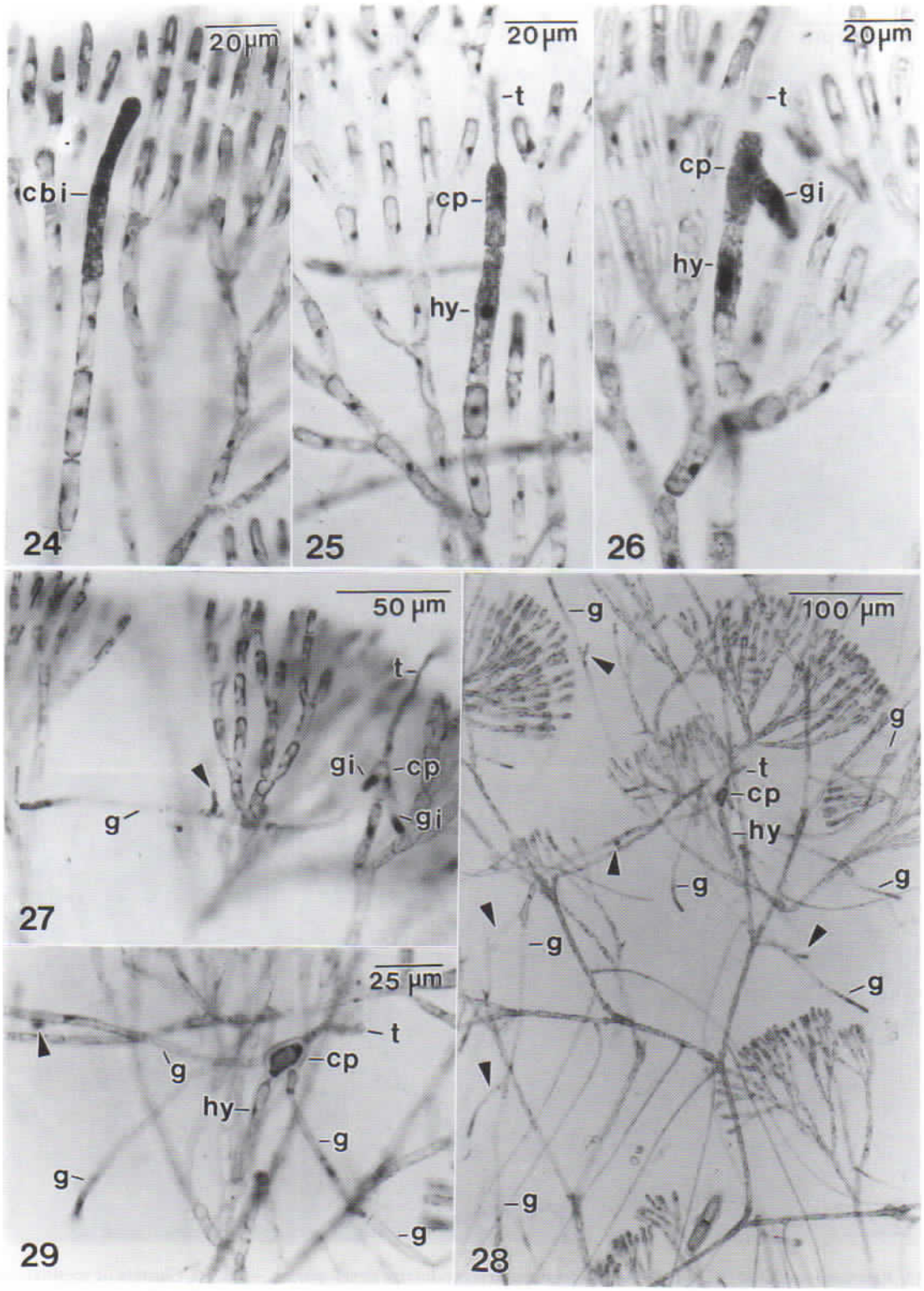
Figs. 7–11. *Renouxia antillana* (#*US-157491*), vegetative morphology, calciferous cells and calcite husks. – Fig. 7, Calciferous cells with blunt (arrowheads) and inflated tips (arrows), surrounded by calcite husks (unstained); – Fig. 8, Calciferous cell containing a fine protoplasmic channel terminated by small cell (arrow), and one devoid of protoplasm with blunt tip (arrowhead; unstained); – Figs. 9–11, After being stained with Wittmann's hematoxylin the calcite has dissolved from the calciferous cells. Note: remnants of disrupted cell wall (arrowheads) partly covering new cell wall of intercalary assimilatory cells; – Fig. 9, Uninucleate calciferous cells with protoplasm-rich tips (arrows); – Fig. 10, Extended rhizoidal filaments (arrows) developed from calciferous cells; – Fig. 11, Assimilatory filaments and intertwined rhizoidal filaments.



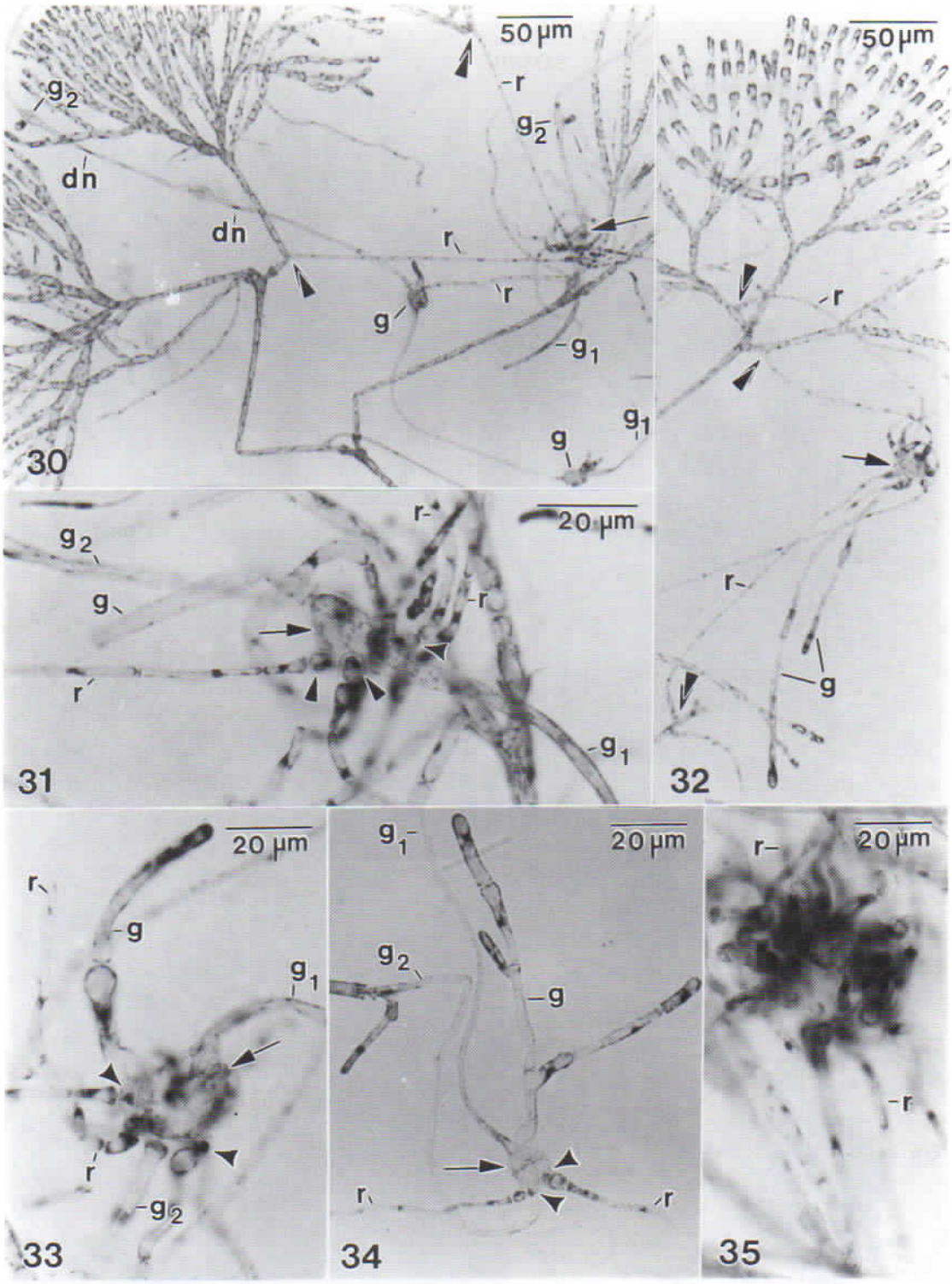
Figs. 12–15. *Renouxia antillana*, vegetative morphology. – Fig. 12, Subterminal cell initiating (arrow) new lateral branch (arrowhead; stained) (#*US-157491*); – Fig. 13, Pseudodichotomously branched assimilatory filaments and initial of secondary branch (arrow; unstained) (#*US-157491*); – Fig. 14, Secondary assimilatory branches initiated thallus outward (arrow; unstained) and inward (arrowheads; unstained) (#*US-157491*). Note: protoplasm-rich calciferous cells with bulbous base; – Fig. 15, Clusters of interconnected assimilatory filaments bearing rhizoidal filaments. Darkly staining cells borne on assimilatory filaments are carpogonial branch initials and young carpogonial branches (#*US-157493*).



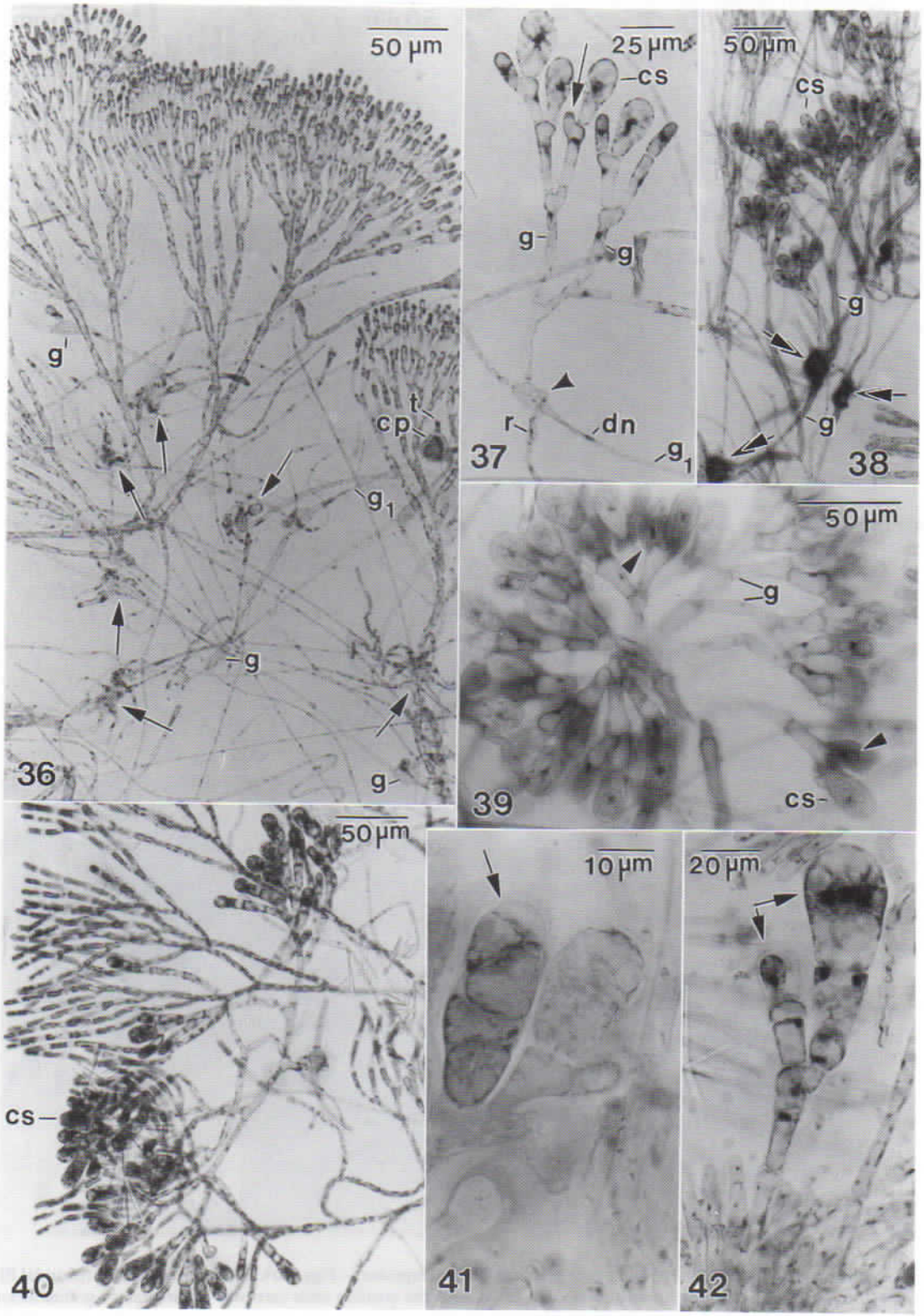
Figs. 16–23. *Renouxia antillana* (#*US-157490*), spermatangial reproductive development. – Fig. 16, Clusters of spermatangial parent cells and spermatangia; – Fig. 17, Subterminal initiation of spermatangial parent cell (arrow); – Fig. 18, Spermatangial parent cells (arrows) borne laterally on subterminal cells of assimilatory filament; – Fig. 19, Spermatangia (arrowheads) cut off by oblique septa from parent cells; – Figs. 20–21, Old clusters of spermatangial parent cells each with remnant spermatangial cell walls (arowheads). – Figs. 22–23, Female pre-fertilization development. Sessile carpogonial branch initials (cbi) and unfertilized carpogonial branches consisting of hypogynous cells (hy) and carpogonia (cp) with straight trichogynes (t) (#*US-157493*).



Figs. 24–29. *Renouxia antillana*, pre- and early post-fertilization development; – Fig. 24, Carpogonial branch initial (cbi), developing as a terminal cell of an assimilatory filament (#*US-157493*); – Fig. 25, Assimilatory filament bearing a two-celled carpogonial branch consisting of hypogynous cell (hy) and carpogonium with trichogyne (t) (#*US-157493*); – Fig. 26, Gonimoblast initial (gi) cut off directly from fertilized carpogonium (cp) with trichogyne (t). The hypogynous cell (hy) is protoplasm-rich with an enlarged nucleus (#*US-157493*); – Fig. 27, Sessile hypogynous cell (hy) and carpogonium (cp) bearing three gonimoblast initials (gi) (one out of focus), and one branching gonimoblast filament (g) (arrowhead). Note persistent trichogyne (t) (#*US-157496*); – Fig. 28, Hypogynous cell (hy), trichogyne (t), and fertilized carpogonium (cp) bearing young gonimoblasts (g) which ramify diffusively among the assimilatory and rhizoidal (r) filaments. Arrowheads indicate initiation of unilateral gonimoblast branches (#*US-157496*); – Fig. 29, Detail of carpogonial branch and gonimoblasts in fig 28.



Figs. 30–35. *Renouxia antillana* (#*US-157496*), post-fertilization development. – Figs. 30–32, Terminal cells of rhizoidal filaments (r) cut off from assimilatory cells (double arrowheads) have fused with the swollen ends (arrows) of intercalary gonimoblast cells (g_1) which in turn have initiated secondary gonimoblast filaments at point of fusion (g). Continuing gonimoblast filaments beyond the swelling are designated g_2. Note the diploid nucleus (dn) is proximal to swollen tips of intercalary gonimoblast cells; – Fig. 31, Detail of fig. 30 showing fusion (curved arrowheads) of terminal rhizoidal cells and swollen tip of an intercalary gonimoblast cell; – Figs. 33–34, Fusion (curved arrowheads) of terminal rhizoidal cells (r) with swollen tip (arrow) of intercalary gonimoblast cell (g_1), and initiation of secondary gonimoblast filaments (g) at point of fusion. The continuing gonimoblast filament is designated g_2; – Fig. 35, Up to 20 rhizoidal filaments (r) may surround a single swollen intercalary gonimmoblast cell.



Figs. 36–42. *Renouxia antillana*, post-fertilization and carposporangial development; – Fig. 36, Overview of interactions illustrated in figs. 28–35 between the rhizoidal filaments and gonimoblast filaments that originated from a single fertilized carpogonium (cp) with a persistent trichogyne (t) (#*US-157496*); – Fig. 37, Carposporangia (cs) formed terminally and laterally from subterminal cell (arrow) on secondary gonimoblast filaments (g). Note the diploid nucleus (dn) (curved arrowhead) proximal to the gonimoblast swelling (g1) which is contacted by a rhizoidal filament (r) (#*US-157496*); – Fig. 38, Secondary gonimoblast filaments originating from swollen primary gonimoblast cells bearing terminal carposporangia (#*US-157492*); – Fig. 39, Secondary gonimoblasts (g) bearing paired terminal carposporangia. Note that secondary carposporangia may be produced successively within multiple walls (arrowheads) (#*US-157492*); – Fig. 40, Clusters of carposporangia (cs) derived from a single gonimoblast swelling; – Fig. 41, Irregularly zonately divided carpotetrasporangium (arrow) (#*US-157494*); – Fig. 42, Multinucleate, multicellular filament (arrows) arising *in situ* (#*US-157494*).

Postfertilization development: A fertilized carpogonium cuts off one (Fig. 26) to four gonimoblast initials which produce septate, hyaline gonimoblast filaments terminated by darkly staining tips (Fig. 27). Fertilized carpogonia are readily recognized among assimilatory cells because the trichogynes persist (Fig. 26), even after the gonimoblast filaments have started to branch (Figs. 27–29, 36). During the earliest postfertilization stages (Fig. 26), the hypogynous cell is rich in cytoplasm and contains the single enlarged nucleus that was present before fertilization. Its contents are depleted gradually as gonimoblast maturation progresses (Figs. 27–29, 36).

The gonimoblast filaments ramify diffusely over a wide area among the assimilatory and rhizoidal filaments (Fig. 28). All gonimoblast cells are elongate with a distal nucleus. Intercalary gonimoblast cells initiate single, small buds laterally (Figs. 27–29) just behind the distal septum. The diploid nucleus of the bearing cell is always situated a short distance behind the bud (Figs. 27–29). Gonimoblast filaments branch unilaterally (Fig. 28). Young gonimoblast filaments are about twice the width of rhizoidal filaments (5–8 μm vs. 2.5–3 μm) and approach the diameter of assimilatory filaments.

The distal ends of some intercalary gonimoblast cells enlarge to a diameter up to 30 μm. After enlargement, rhizoidal filaments grow towards an enlarged end and each cuts off one or two small cells that fuse with the gonimoblast cell (Figs. 30–35). These rhizoidal cells fuse only partly with the enlarged portion of a gonimoblast cell, and their nuclei remain in the unfused portion (Figs. 31, 33). Upon fusion, the rhizoidal cell nuclei degenerate (Fig. 34) and rhizoidal and gonimoblast nuclei do not intermix. Up to twenty rhizoidal filaments may surround a single swollen end of an intercalary gonimoblast cell (Fig. 35). Extensive interactions between rhizoidal and gonimoblast filaments across a wide area can be traced back to a single fertilized carpogonium (Fig. 36).

A single secondary gonimoblast filament is produced from the enlarged portion of each gonimoblast cell with which the terminal rhizoidal cells have fused (Figs. 30–34, 36). The terminal cells of secondary gonimoblast filaments mature into carposporangia and a new carposporangium is initiated as a bulge from a subterminal gonimoblast cell (Fig. 37) which subsequently septates. Carposporangia are formed in terminal, pseudodichotomous pairs, often forming dense clusters (Figs. 38–40). Carposporangia are encased in a thickened cell wall 1–2 μm wide and each typically measures 10–20 μm broad and 30–35 μm long (Figs. 38–40). Secondary carposporangia are produced successively within the empty carposporangial walls that remain following release of the carpospores (Fig. 39). Most carpospores are released. In ten instances, carposporangia were found that contained four, irregularly zonately arranged spores (Fig. 41). A few carpospores germinated *in situ* into iregular, multinucleate filaments (Fig. 42).

Discussion

Vegetative development: In 1989, Norris and Bucher described an unusual red algal genus, *Rhodogorgon*, from the Caribbean. This is the only alga other than *Renouxia* that has calciferous cells enclosed by brown calcite husks as shown by powder X-ray diffraction analysis [18; I. Macintyre, pers. comm.]. The only other red algae which deposit calcite are the Corallinales [12]; in all other calcified Rhodophyta calcium carbonate is deposited as aragonite [e.g., 16, 28].

The calciferous cells in *Renouxia* are initially protoplasm-rich and uninucleate, containing a single nucleus. They may become enucleate and apparently devoid of protoplasm, presumably as a result of breakdown. This observation is in agreement with accounts of the fine structure studies of calciferous cells of *Rhodogorgon* by Pueschel, Eichelberger and Trick [25].

Although the calciferous cells of *Renouxia* differ from those of *Rhodorgorgon* [18, 19, 24, 25] in their position and the extent of their calcium carbonate coating, they are homologous to them. The positional differences can be accounted for by differences in the growth pattern of the assimilatory filaments.

The role of calciferous cells in *Rhodogorgon* is unknown [18, 24, 25]. Norris and Bucher [18] speculated that the cells may be involved in secondary branch formation, play a role in nutrient boundary layer breakdown, or are possibly herbivore deterrents. In this study, we have discovered that in *Renouxia* the calciferous cells can be initials of the rhizoidal filaments. The husks in *Renouxia* evidently dissolve as soon as the calciferous cells have initiated rhizoids more than two cells long. We now interpret fig. 28 in Norris and Bucher [18] as showing a calciferous cell in *Rhodogorgon* that has divided once, resulting in a terminal cap cell similar to the one illustrated in *Renouxia* (Fig. 8). We disagree with Ogden [19, p. 474] that the septum in fig. 28 in Norris and Bucher [18] is an "enlarging chloroplast."

Growth in *Rhodogorgon* has been interpreted as apparently being pseudomultiaxial [18], or multiaxial [19, 25]. We disagree with the interpretation of Ogden [19] that there are axial filaments in *Rhodogorgon* and that they exhibit cellulosympodial growth. We interpret the "axial filaments" *sensu* Ogden [19, figs. 2–3] as being assimilatory filaments that initiate lateral branches monopodially. A cluster of apical initials and axial filaments that maintain growth as found in multiaxial taxa ("Springbrunnentypus" or fountain type of Oltmanns [20]) is absent in both *Renouxia* and *Rhodogorgon*. Although thalli of *Renouxia* are gelatinous, flaccid and appear to be undifferentiated into cortical and medullary tissues, and those of *Rhodogorgon* are cartilaginous and seem to be differentiated into a sharply demarcated zone of cortical fascicles and dense medulla (see fig. 8 in Norris and Bucher [18]), we have found on re-examination that the fundamental growth pattern of *Rhodogorgon* is basically the same as that of *Renouxia*. Thalli of both genera lack a defined meristem and consist entirely of laterally connected masses of assimilatory filaments bearing rhizoidal filaments. Typical cortical and medullary tissues are absent. The central region of *Rhodogorgon* superficially resembles the medulla of certain Galaxauraceae (Nemaliales), but as Coomans and Hommersand [2] have shown, the thalli are multiaxial

Table 1. Comparison of vegetative characters between *Renouxia* and *Rhodogorgon*.

	Renouxia	*Rhodogorgon*
Habit	Thallus flaccid, gelatinous; lobed	Thallus cartilaginous; terete main axes and branches
Anatomy	Loosely interwoven assimilatory filaments & thin-walled rhizoidal filaments	Compact, fasciculate assimilatory filaments & thick-walled rhizoidal filaments
Assimilatory filament branching	Indeterminate; typically pseudodichotomous	Determinate, in fascicles; typically pseudotrichotomous
Apical cells	Dome-shaped; densely pigmented	Becoming inflated; hyaline
Cell walls of intercalary cells	Disrupted	Intact
Calciferous cells	Sessile; scattered, 5–6 orders of branches below surface	Pedicellate; restricted to basal cells of cortical fascicles
Calcite husks	Surround calciferous cells completely	Surround calciferous cells distally

in the Nemaliales and axial filaments develop sympodially. Besides the greater thickness and density of the rhizoidal filaments in *Rhodogorgon*, the chief difference between *Rhodogorgon* and *Renouxia* lies in the position, extent and branching pattern of the assimilatory filaments (Table 1). In *Renouxia* the assimilatory filaments exhibit indeterminate branching with the branches predominantely unilateral and pseudodichotomous; in *Rhodogorgon* they are determinate and predominantly pseudotrichotomously branched (see figs. 10–13 in Norris and Bucher [18]) forming short fascicles (see figs. 8–13 in Norris and Bucher [18]).

The apical cells of assimilatory filaments are dome-shaped when actively dividing and afterwards become inflated and hyaline in *Rhodogorgon* (see figs. 10, 11, 16, 18, 23–26 in Norris & Bucher [18]; see also TEM observations by Pueschel, Trick & Norris [24] figs. 1, 2, 5, 6). By contrast, apical cells in *Renouxia* remain pigmented, dome-shaped, and retain the capacity to divide indefinitely (Fig. 12).

Terminal and intercalary cells of assimilatory filaments in *Rhodogorgon* are commonly surrounded by multiple spreading layers of wall material [see figs. 18–20 in Norris & Bucher [18]; and figs. 8–10 in Pueschel, Trick & Norris [24]). *Renouxia*, however, is unique in that intercalary assimilatory cells are surrounded by thick cell walls that are ruptured in the course of cell elongation. There is no indication that intercalary divisions have taken place, and mitotic division figures with spindles in equatorial plane were never observed. This type of cell elongation in which the outer cell walls rupture while the inner wall extends has not previosuly been reported in red algae. This unusual mode of cell elongation is also absent in *Rhodogorgon*, presumably because the thallus does not expand indefinitely in diameter, and because the assimilatory filaments mature and cease meristematic activity.

Reproductive development: In the Florideophycidae, carpogonial branches are either initiated terminally or laterally on a vegetative filament [e.g., 11, 15]). In *Renouxia*, both situations occur (Figs. 23, 24). Carpogonial branch initials are transformed from the apical cells of secondary filaments which arise inside a cluster of assimilatory filaments. We interpret the carpogonial branches of *Renouxia* as being two-celled, since only the carpogonium and hypogynous cell are morphologically and cytologically modified (Fig. 25). Should transformation take place when the initial is only one cell long, the carpogonial branch will be lateral and sessile. Prior to initiation of a trichogyne on a carpogonium, the hypogynous cell in *Renouxia* becomes darkly stained and its nucleus enlarges. Presumably these enlarged nuclei (Fig. 26) have elevated levels of DNA or RNA that code for proteins as Hommersand and Fredericq [11] have postulated for other red algae.

Fertilization is evidently rare in *Renouxia* since many unfertilized carpogonia degenerate. The cytoplasm and cell walls of such non-functional carpogonia frequently deteriorate, leaving only the hypogynous cell and remnant pit connection that formerly linked it to the carpogonium.

Ogden [19] recently reported the female reproductive system of *Rhodogorgon*. The carpogonium is sessile and lateral on an assimilatory filament and bears a straight trichogyne. Ogden [19] stated that the carpogonium may be cut off occasionally from a "medullary" filament. Based on our own observations of *Rhodogorgon*, the figures 11, 13 and 15 in Ogden [19] represent sessile unfertilized car-

pogonia that have undergone septation from the bearing assimilatory cell. Furthermore, what Ogden [19, fig. 15] interpreted as a "gonimoblast filament initial" is instead a newly formed lateral vegetative cell.

In the Florideophycidae, sporangia-bearing gonimoblast filaments are initiated either directly from fertilized carpogonia, or indirectly from auxiliary cells into which the fertilization nucleus (or its derivatives) have been transferred [4]. In *Renouxia*, gonimoblasts are produced directly from carpogonia, a condition also shared by some members of the Acrochaetiales, Batrachospermales, and Nemaliales, all of which lack secondary pit connections. There are, however, significant differences in the female reproductive system of *Renouxia* and those of these three orders (Table 2). Fertilized carpogonia do not divide in *Renouxia* but give rise directly to gonimoblast filaments which branch diffusely through the surrounding vegetative filaments, as in some species of *Thorea* (Thoreaceae, presently in the Batrachospermales) [32] and *Dermonema* (Liagoraceae, Nemaliales) [31]. Diffusely branched gonimoblast filaments bearing carposporangia are also present in *Rhodogorgon*; however, only the gonimoblast initials have been identified, and a connection between carpogonia and mature gonimoblast filaments has not, so far,

Table 2. Comparison between Rhodogorgonales, Acrochaetiales, Batrachospermales and Nemaliales.

	Rhodogorgonales	Acrochaetiales	Batrachospermales	Nemaliales
Distribution	Marine	Most marine; few freshwater	Freshwater	Marine
Growth	Diffuse, embedded in matrix	Diffuse, not embedded in matrix	Uniaxial & multiaxial	Multiaxial, sympodial
Pit plug with enlarged outer cap layers	+	+/−	+	−
Calciferous cells	+	−	−	−
Calcite	+	−	−	−
Carpogonial branch	2-celled; or only carpogonium	-; or only carpogonium	-; or > 3-celled	3 or more celled
Auxiliary cell	−	−	−	−
Sterile cells/filaments on carpogonial branch	−	−	+/−	+/−
Sterile cells/filaments adjacent to carpogonial branch	−	−	−	+/−
Initiation of gonimoblasts from undivided carpogonium	+	+/−	+	−/+
Gonimoblasts diffusely branched	+	−	−/+	−/+
Carpogonial branch fusion cell	−	−	+/−	+/−
Fusion between gonimoblasts & vegetative cells	+	−	−	−
Monosporangia	−	+	+	+
Tetrasporangia	−	Cruciate	−	Cruciate
Carpotetrasporangia	Irregularly zonate carpotetrasporangia?	−	−	−/+

Key to terms: (+) = presence; (−) = absence; (+/−) = presence in most families; (−/+) = absence in most families.

been seen [see 19; pers. obs.]. Although Ogden [19, fig. 14] states that "diffuse gonimoblast filamens are formed up through the carpogonium" in *Rhodogorgon*, in our opinion, the illustration shows part of a gonimoblast filament lying underneath assimilatory filaments. We have observed gonimoblast initials formed directly from the carpogonium in this species (#JN–16241, US).

In most other red algae gonimoblast formation is mediated by one or more auxiliary cells. Only in some Gigartinales (including the Cryptonemiales *sensu* Kraft and Robins [14]) do carpogonia produce connecting filaments that initiate gonimoblasts directly in the proximity of auxiliary cells, or fuse with one or more auxiliary cells which in turn give rise to gonimoblasts [e.g., 11, 21]. Drew [4] interpreted the connecting filaments that originate from the carpogonia as primary gonimoblasts and those formed after fusion with an auxiliary cell as secondary gonimoblasts. Although auxiliary cells and connecting filaments are absent in *Renouxia*, the gonimoblasts that issue from the carpogonium resemble the septate, branched connecting filaments found in some Gigartinales, for example, the Calosiphoniaceae and Gymnophlaeaceae [15]. The similarities are striking. The enlarged ends of an intercalary gonimoblast cell [in *Renouxia*] resembles an auxiliary cell, whereas the proximal filament simulates an incoming connecting filament, and the continuing filament an outgoing connecting filament (Figs. 31, 34). Like the auxiliary cells of some nonprocarpic Gigartinales, the swollen gonimoblast cells of *Renouxia* have both a nutritive and generative function. Auxiliary cells are an integral part of a system of vegetative filaments to which nutriment may be channeled directly [11]. In contrast, the nutritive function of the swollen gonimoblast cells depends on the directed growth and fusion of numerous rhizoidal filaments derived from calciferous cells situated in the interior of clusters of assimilatory filaments. Like some types of auxiliary cells, the swollen gonimoblast cells each produce a single initial which, in the case of *Renouxia*, bear branched gonimoblast filaments terminated by pairs of carposporangia. Interestingly, the diploid nuclei of intercalary cells remain proximal to their swollen ends at the time of the rhizoidal fusions, thus preventing mixing of haploid and diploid nuclei. This spatial separation between nuclear types is common in auxiliary cells of red algae, in which haploid auxiliary cell nuclei frequently degenerate after the entry of diploid fertilization nuclei [11]. Whereas auxiliary cells and swollen gonimoblast cells are clearly non-homologous structures, they are both modified for similar function: that of increasing the reproductive potential by amplifying the number of carpospores produced from a single fertilization [see 27]. Among those genera of red algae that have diffusely branched gonimoblasts, only in *Renouxia* are vegetative cells known to initiate the fusion process with them.

We interpret the "monosporangia" illustrated in Ogden [19, figs. 20–23] for *Rhodogorgon* to be carposporangia on ramifying gonimoblast filaments. Carposporangia in *Renouxia* occasionally divide to produce four cells in an irregularly zonate arrangement, suggesting that they may function as tetraspores (carpotetraspores *sensu* Guiry [6, 7]). All carpotetrasporangia reported in the Nemaliales are irregularly cruciately divided [7, 8]. Some carposporangia in *Renouxia* appear to germinate *in situ*, producing irregular filaments composed of uni-and multinucleate cells, and the 4-celled stage we have described may be part of this process. Karyological data are not available. Ogden [19, p. 475] also observed similar carpospores germinating *in situ* in *Rhodogorgon*.

Successive production of carposporangia, as seen in *Renouxia* and *Rhodogorgon* [19, figs. 16–18; pers. obs.], is common in species of Florideophycidae regarded as being primitive [7]. Gabrielson and Garbary [5] concluded that this feature may prove diagnostic for the Acrochaetiales, Nemaliales and Bonnemaisoniales. Maggs and Guiry [17] also reported this condition in a species of *Gelidiella*, suggesting that it may be more widespread than previously thought. Multiple concentric walls enveloping carposporangia, spermatangia and even vegetative cells in *Renouxia* and *Rhodogorgon* are homolgous structures, otherwise found only in primitive orders of the Florideophycidae.

Taxonomic relationships: The classification of red algae is based predominantly on the developmental morphology of the female reproductive system (e.g., 3, 15, 26). More recently, the ultrastructural characters of pit connections have been found useful for distinguishing taxa at ordinal rank [see 22, 23].

Primitive Florideophycidae are characterized by the presence of monosporangia, spermatangia, carposporangia or tetrasporangia on unmodified branched filaments that are very similar in appearance [7, 11]. In *Renouxia* and *Rhodogorgon* the initiation of both lateral vegetative branches, gonimoblast filaments, spermatangial parent cells, and carposporangia are all similar and follow the same growth pattern.

Norris and Bucher [18] noted that *Rhodogorgon* is similar to *Thorea* and *Nemalionopsis* (Thoreaceae, presently in the Batrachospermales) in certain respects, and on the basis of pit plug morphology, Pueschel, Trick and Norris [24] tentatively referred *Rhodogorgon* to the Batrachospermales. *Renouxia* also possesses similar pit plugs with two cap layers in which the outer cap layer is enlarged and dome-shaped (Pueschel, pers. comm.). Several characters exclude *Renouxia* and *Rhodogorgon* from the Batrachospermales. Genera currently placed in the Batrachospermales are exclusively freshwater, have compact gonimoblasts, and are uncalcified. Curently up to twenty-one orders of Rhodophyta are recognized [30]. Based on morphological evidence presented in this study, *Renouxia* and *Rhodogorgon* differ markedly from any of these orders (Table 2). They share pit plug morphology with some members of the Acrochaetales and Batrachospermales; however, they possess a unique cell type, the calciferous cell surrounded by a calcite husk, and have evolved a distinctly different reproductive strategy found nowhere else among the red algae. Finally, although members of the Corallinales also have a dome-shaped pit plug morphology [23] and calcite [28], there are significant differences in vegetative and reproductive morphology and development of *Rhodogorgon* and *Renouxia* that exclude a close phylogenetic relationship [see also 18].

Taxonomic Conclusions

Renouxia Fredericq et J. Norris, gen. nov.

Diagnosis: Thallus flaccidus, gelatinosus, lobatus. Ramificatio indeterminata, laxe, uniseriata ex filis assimilatoribus pseudodichotomibus et filis rhizoidalibus tenuiparietibus. Cellulae intercalaria plerumque tectae parietibus veteribus partim. Cellulae apicalia pigmentosae tholiformia. Cellulae calciferae sessilia, brevia, tectae omnino aut cylindris calcareis, extensiae in fila rhizoidalia, dispersiae lateralia insidentia filis assimilatoribus sub supremis quadriordinibus ramificationis. Gametophyti feminei et masculini diclini. Carpogonia conica. Nonnula initia gonimoblasti orta e carpogonia, ramificantia diffusa unilateralia. Cellulae terminalia filorum rhizoidalium conjunctae cellulis gonimoblasti intercalaribus unde plus fila gonimoblasti orta ferentia fasciculos terminales carposporangiorum. Carpotetrasporae? zonatae divisae irregulariter et fila multinucleata orta in situ carposporangiis.

Description: Thallus flaccid, lubricous, lobed, composed of loose masses of interconnected assimilatory filaments bearing thin-walled rhizoidal filaments. Branching of assimilatory filaments indeterminate and pseudodichotomous. Intercalary assimilatory cells surrounded by disrupted outer cell walls. Apical cells dome-shaped, densely pigmented. Calciferous cells short, completely surrounded by calcite husks, scattered and borne laterally on assimilatory filaments below the uppermost 5–6 orders of branches, and may extend into rhizoidal filaments. Male and female gametophytes on separate thalli. Carpogonia conical. Diffusely branched gonimoblast filaments formed directly from fertilized carpogonium, ramifying unilaterally among assimilatory and rhizoidal filaments. Terminal cells of rhizoidal filaments fusing with enlarged ends of intercalary gonimoblast cells, from which secondary gonimoblast filaments develop that bear terminal pairs of carposporangia. Irregularly zonately divided sporangia (carpotetrasporangia?) and few-celled, multinucleate filaments developing in situ within carposporangia.

Unispecific.

Type: *Renouxia antillana* Fredericq et J. Norris (herein).

Renouxia antillana Fredericq et J. Norris, sp. nov.

Diagnosis: Thallus rosealus, 2 usque ad 5 cm non pressatus, lobatus saepe projectoribus obtusis, per hapteron discoideum affixus. Stipes brevis, ad 3 mm lat. Cellulae intercalaria 5–8 μm lat. × 15–25 μm long., apicalia tholiformia; cellulae calciferae 4–8 μm lat. × 20–25 μm long., etumidapiculatae vel tumidapiculatae, protoplasmicae vel eprotoplasmicae; cylindri calcarei 12–15 μm long. × 25–50 μm lat.; filorum rhizoidalium cellulae tenuiparietes 2.5–3 μm lat. Cellulae parentes spermatangiorum 2–3 μm lat. × 9–12 μm long.; spermatium 2–3 μm lat. Initium fili carpogonialis 8 μm lat. × usque ad 50 μm long.; filum carpogoniale 40–60 μm long.; cellula hypogyna 8 μm lat. × 25–45 μm long.; carpogonium 8 μm lat. × 20 μm long. Fila gonimoblasti 5–8 μm lat., partes amplificatae cellularum gonimoblasti usque as 15–30 μm lat. Carposporangia 10–20 μm lat. × 30–35 μm long. Carpotetrasporangium 15 μm lat. × 35 μm long.

Description: Thallus light-pink, 2–5 cm wide and up to 5 cm tall, consisting of few to many broad lobes which often bear blunt projections, giving the surface a ruffled appearance; attached to substrata by a discoid holdfast. Stipe short, to 3 mm wide. Thallus composed of assimilatory filaments bearing calciferous cells and rhizoidal filaments. Intercalary assimilatory cells 5–8 μm broad, 15–25 μm long, terminating in dome-shaped apical cells, 5 μm broad, 15–25 μm long; calciferous cells 4–8 μm broad, 20–25 μm long, with inflated or blunt tips; calcite husks 12–15 μm broad, 25–30 μm long; rhizoidal filaments composed of thin-walled cells 2.5–3 μm broad. Spermatangial parent cells 2–3 μm broad, 9–12 μm long; spermatia 2–3 μm diam. Carpogonial branch initials 8 μm broad, reaching 50 μm in length; 2-celled carpogonial branches (excluding trichogyne) 40–60 μm long; hypogynous cells 8 μm broad, 25–45 μm long; carpogonia 8 μm broad, 20 μm long. Gonimoblast filaments 5–8 μm broad, enlarged ends of intercalary gonimoblast cells reaching 15–30 μm in width. Carposporangia 10–20 μm broad, 30–35 μm long. Carpotetrasporangia? 16 μm broad, 35 μm long.

Holotype: Alg. Coll. #*US*-157157, spermatangial specimen, Ilet à Caret (between Grande Terre and Basse Terre), Grand Cul de Sac Marin, Guadeloupe, 3 Apr 90, leg. S. Fredericq & S. Mège.

Isotypes: Spermatangial specimens – Alg. Coll. #*US*-157490 & #*US*-157491; and MEL, MICH, NCU and UC.

Paratypes: Ilet à Caret, Grand Cul de Sac Marin, Guadeloupe, all leg. S. Mège: Alg. Coll. #*US*-157492, spermatangial specimens, 1 May 90, and Alg. Coll. #*US*-157494, spermatangial specimens, 15 May 90; and a carposporangial specimen, Alg. Coll. #*US*-157493, 24 May 90.

Ilet à Fajou, Passe à Cola, Grand Cul de Sac Marin, Guadeloupe, 31 Mar 91, leg. S. Mège: Alg. Coll. #*US*-157495, spermatangial specimens; and Alg. Coll. #*US*-157496, carposporangial specimens.

Distribution: Caribbean Sea-Guadeloupe, Lesser Antilles; and Jamaica, Greater Antilles.

Etymology: We are naming the new genus *Renouxia* in honor of Dr. Aline Renoux, the phycologist at the Université Antilles-Guyane, Pointe à Pitre, Guadeloupe, who lent her support and enthusiasm to this study.

Rhodogorgonaceae Fredericq, J. Norris et Pueschel, fam. nov.

Diagnosis: Thalli variantes forma, lubrici. Anatomia compacta vel laxe, cum vel sine limite inter fila corticalia et rhizoidalia. Incrementum apicalis diffusa; ramificatio indeterminata pseudodichotomata, aut fasciculata, determinata pseudotrichotomataque. Fila lateralia formata ubi cellulae intercalares protrusae partem cytoplasmii septataeque. Fila rhizoidalia tenueparieta aut crassiparieta. Cellulae apicalia pigmentosae tholiformia, aut inflatae hyaline. Cellulae calciferae sessilia aut pedicellate, tectae omnino aut partim cylindris calcareis. Fasciculatae cellulae parentes spermatangiorum cellulae subterminali filorum corticalium ortae, spermatangio singulo ferentes. Filum

carpogoniale constans ex cellula hypogyna elongata nucleo amplificato et carpogonio distali cum trichogyna stricta persistenti.

Description: Thalli of various forms, slippery, compact or loose, with or without sharp demarcation between assimilatory filaments and rhizoidal filaments. Branching of assimilatory filaments indeterminate and pseudodichotomous, or fasciculate, determinate and pseudotrichotomous. Rhizoidal filaments thin-walled or thick-walled. Apical cells pigmented and dome-shaped, or inflated and hyaline. Calciferous cells sessile or pedicellate, partly or completely surrounded by calcite husks. Spermatangial parent cells produced in small subterminal clusters. Unfertilized female reproductive structures either 2-celled carpogonial branches, each consisting of elongated hypogynous cell with an enlarged nucleus and carpogonium (*Renouxia*), or solitary carpogonia (*Rhodogorgon*).

The Rhodogorgonaceae contains two genera, *Rhodogorgon* and *Renouxia*.

Type: *Rhodogorgon* J. Norris et Bucher (1989, p. 1053).

Rhodogorgonales Fredericq, J. Norris et Pueschel, ord. nov.

Diagnosis: Thallus uniseriatus ex filis corticalibus interconnectis, et filis rhizoidalibus oblongatis eramosis constans. Extensio specialis cellularum calcifera orta cellulis corticalibus, tecta cylindris calcareis (calcite). Fila rhizoidalia septata e cellulis calciferibus evoluta aut cellulis interioralibus corticalibus. Cellulae vegetativae uninucleatae, synapsibus secundis absentibus. Synapses primariae obturamentae cum duobus stratis capitularibus continentes, exterioribus tholiformibus. Initium ramuli carpogonialis sessile aut cellula terminalis fili corticalis. Ramuli carpogoniales 2-cellulares. Cellulae auxiliares et fila connectentia absentia. Nonnula initia gonimoblasti orta e carpogonia, ramificantia diffusa unilateralia sine conjunctionibus cum cellulis vegetativis. Cellulae terminalia filorum rhizoidalium sive non conjunctae cellulis gonimoblasti intercalaribus unde plus fila gonimoblasti orta. Fila gonimoblasti ferentia, fasciculos terminales carposporangiorum formantes sympodiales. Carpotetrasporangia? et fila multinucleata sive non orta in situ carposporangiis.

Description: Defined meristem absent; thalli not differentiated into typical cortex and medulla but composed of interconnected assimilatory filaments bearing rhizoidal filaments. Localized calcite husks surrounding specialized, thin-walled calciferous cells. Rhizoidal filaments septate, sometimes developing from calciferous cells. Pit plugs with two cap layers, outer cap layer an enlarged dome. Vegetative cells uninucleate, secondary pit connections absent. Carpogonia or carpogonial branch initials sessile, or transformed terminal cells of secondary filaments. Carpogonial branches 2-celled. Carpogonia with straight trichogyne. Auxiliary cells and connecting filaments absent. Gonimoblast initials formed directly by fertilized carpogonium. Gonimoblast filaments diffusely branched, ramifying unilaterally among assimilatory and rhizoidal filaments without establishing fusions. Terminal cells of rhizoidal filaments facultatively fusing with intercalary gonimoblast cells, from which additional gonimoblast filaments are initiated, or theses stages currently unknown.

Unifamilial.

Type: Rhodogorgonaceae Fredericq, J. Norris et Pueschel (herein).

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Key words: Calcite, Lesser Antilles, Marine Algae, morphology, *Renouxia*, *Rhodogorgon*, Rhodogorgonaceae, Rhodogorgonales, Rhodophyta, taxonomy

Suzanne Fredericq and James N. Norris, Department of Botany, Duke University, Durham, North Carolina 27708–0338; and Department of Botany, NHB 166, National Museum of Natural History, Smithsonian Institution, Washington D.C. 205660.