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RHODOGORGON, AN ANAMOLOUS NEW RED ALGAL GENUS FROM THE CARIBBEAN SEA

James N. Norris and Katina E. Bucher

Abstract.—*Rhodogorgon* (Rhodophyta) a new genus with two species, *R. carriebowensis* and *R. ramosissima,* superficially resembling some gorgonian soft corals, is described from the Caribbean Sea. Studies of vegetative morphology, male reproductive structure, pigment composition, nature of calcium carbonate, and ultrastructure reveal a combination of characters that is exceptional among the red algae: thallus with a sharply demarcated cortex of laterally interconnected cortical fascicles and rhizoidal filamentous medulla; three types of cortical cells which develop from the base of a cortical fascicle—1, pigmented, assimilatory filaments with inflated, hyaline apical cells, 2, unusual elongate, hyaline, hair-like calciferous cells with inflated tips, and 3, basal hair cells; uninucleate vegetative cells that lack secondary pit-connections and cell fusions; pit-plugs with two cap layers on either side of plugs, the outer caps dome-shaped; and calcite (among the red algae previously known only in the Corallinales) confined to single "husklike" structures (unique among all algae) that distally surround a calciferous cell. Thalli are apparently dioecious; spermatangial parent cells are borne bilaterally on subterminal cells of the cortical filaments, with each cutting off a single spermatangium by oblique division. Possible taxonomic affinities of the new genus are discussed.

A relatively large, cartilaginous, and peculiar red alga has been collected at many Caribbean localities over the past 16 years. Plants are usually rare or sparse in occurrence and grow in shallow to mid-subtidal depths on rocks or coral heads, in patch reefs, fringing reefs and barrier reefs throughout the year. This alga could have been easily overlooked because of its resemblance to some gorgonians (Gorgonacea; Anthozoa) in shape, color, and thick cartilaginous texture (see color photograph of "mystery alga" in Littler et al. 1989:184). It has been noted by F. M. Bayer (octocoral systematist) that the living plants of *Rhodogorgon carriebowensis* superficially resemble some species of *Carijoa* F. Müller (a gorgonian cosmopolitan in subtropical-tropical oceans), and the dried herbarium specimens of *R. ramosissima* resemble *Plumigorgia* Nutting (a gorgonian from the Indo-Pacific). Initial examination by our phycological colleagues suggested specimens could be confused with gorgonians. The presence of pit plugs between the exceedingly small cells, documented by TEM studies (S. Brawley, pers. comm.), demonstrated that the specimens were plants!

Materials and methods.—Specimens were collected from the Caribbean Sea, from 1973 to 1989 by skin or SCUBA diving, at depths from 1–25 m. For morphological studies, thalli were pressed fresh or preserved in 5% buffered Formalin/seawater. Collection numbers cited with the prefix JN- or KB- refer to the field notebooks of J. N. Norris or K. E. Bucher, respectively. Live specimens were studied in the field at the Smithsonian Institution's Carrie Bow Cay Laboratory on the barrier reef of Belize, the Galeta

Marine Laboratory of the Smithsonian Tropical Research Institute (STRI) on the Caribbean coast of the Republic of Panama, and aboard the NSF ships OR/V *Cape Florida* and OR/V *Columbus Iselin.*

Microscope slides for anatomical studies were prepared from living or liquid-preserved specimens by hand sectioning with single- or double-edged razor blades, or by using a Reichert Histostat cryostat microtome to make both transverse and longitudinal sections of the main axes, branches and apices. Some were acidified with 2–5% HCL to remove calcium carbonate, and then stained with aniline blue and mounted in serial dilutions of clear Karo Syrup with phenol added (as a preservative) following techniques of Tsuda and Abbott (1985), or acidified with 1–5% acetic acid and stained with aceto-iron-hematoxylin-chloral-hydrate (Wittmann 1965) and mounted in 50: 50 Hoyer's mounting medium according to the procedure of Hommersand and Fredericq (1988). Other preparations of fresh or liquid-preserved specimens were not acidified or stained prior to mounting on microscope slides in order to observe the unique calciferous cells.

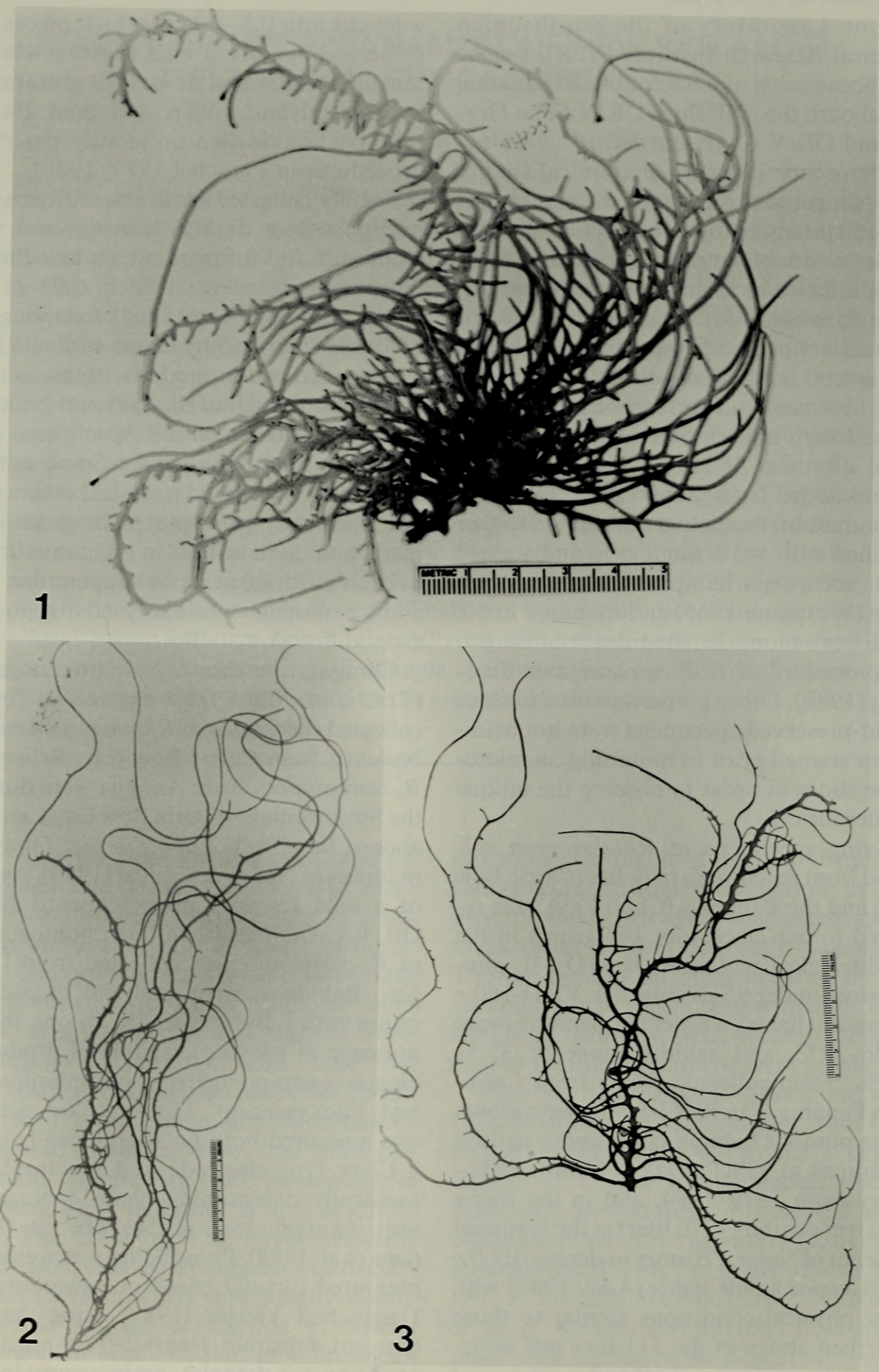
Living specimens of *Rhodogorgon* collected from patch-reefs in Belize (Carrie Bow Cay) and the Bahamas (Chub Cay) were returned to our laboratory and grown in the 511-liter algal reef tank, at 11D:13L photoperiod (under 6 Sylvania, 6 ft. VHO-160w fluorescent lights), a water temperature range of 26–29°C, and salinity range of 35.5–36.7‰. Field collected plants from Caribbean Panama (San Blas Islands) were grown in the outdoor holding tanks under natural conditions at STRI's Galeta Marine Laboratory from 1979–1984, and in the living coral reef exhibit (7570 liter) at the National Museum of Natural History under ten-1000w multi-vapor halide lights (Adey 1983) with other physical conditions similar to those described above in the 511 liter reef tank.

For ultrastructure studies, branches and main axes of freshly collected specimens were cut into 0.5–1.0 mm thick pieces and preserved in 5 dram vials of either 4% glutaraldehyde/seawater or 4% glutaraldehyde/cacodylate buffer, and then 2% osmium tetroxide (see previously described procedures in Pueschel 1979, 1980).

Freshly collected plants were frozen and transported in dark bottles covered with aluminum foil for pigment studies. Phycobiliproteins were extracted in 0.03 *M* Potassium-phosphate (pH 6.8) following the methods described by Gantt et al. (1979).

For calcification analysis, trans-sections 0.3–0.5 mm thick of the axes and branches of living and preserved specimens were placed on microscope slides. Some sections were rinsed in distilled water and others were not, then they were placed in glass petriplates and dried at 40°C in a Thomas drying oven or air-dried at room temperature. Calcium carbonate was analyzed by powder x-ray diffraction studies.

Comparative thin-layer chromatograms (TLC's) of 90% ETOH extracts of freshly collected specimens of *Rhodogorgon carriebowensis* from Carrie Bow Cay, Belize and *R. ramosissima* from Antigua were done at the Smithsonian's Carrie Bow Cay Lab. and aboard the OR/V *Cape Florida,* following methods of Norris & Fenical (1985). As part of a field research project aboard NSF's OR/V *Columbus Iselin* fresh homogenates of *R. carriebowensis,* collected from Chub Cay, Bahamas, were analyzed in collaboration with J. Burgess and R. Jacobs, for the presence of enzymes capable of producing bioactive compounds (i.e., phospholipase A and lipoxygenase). Lipoxygenase activity was measured both polarigraphically using a Clark type electrode and spectrophotometrically determining olefin conjugation utilizing arachidonic acid as substrate (Reddana et al. 1988). Phospholipase activity was measured directly based on procedures of Dagan and Yedgar (1987) using the fluorescent substrate 1-acyl-2-(N-4-nitrobenzo-2-oxa-1,3-diazole) aminocaproylphosphatidycholine, and separating the free fatty



Figs. 1–3. *Rhodogorgon carriebowensis,* from Carrie Bow Cay, Belize. 1, Holotype (US-098360). 2, A long, lax form with branches to 40 cm in length (US-098364). 3, A loose, lax form (US-098363).

acid product by solid phase extraction on C_{18} cartridges.

Type specimens, including microscope slides and liquid preserved material are deposited in the Algal Collection of the U.S. National Herbarium, National Museum of Natural History, Smithsonian Institution. Additional cited specimens are deposited in ADU, BISH, MELU, MICH, UC and US (following herbarium designations of Holmgren et al. (1981).

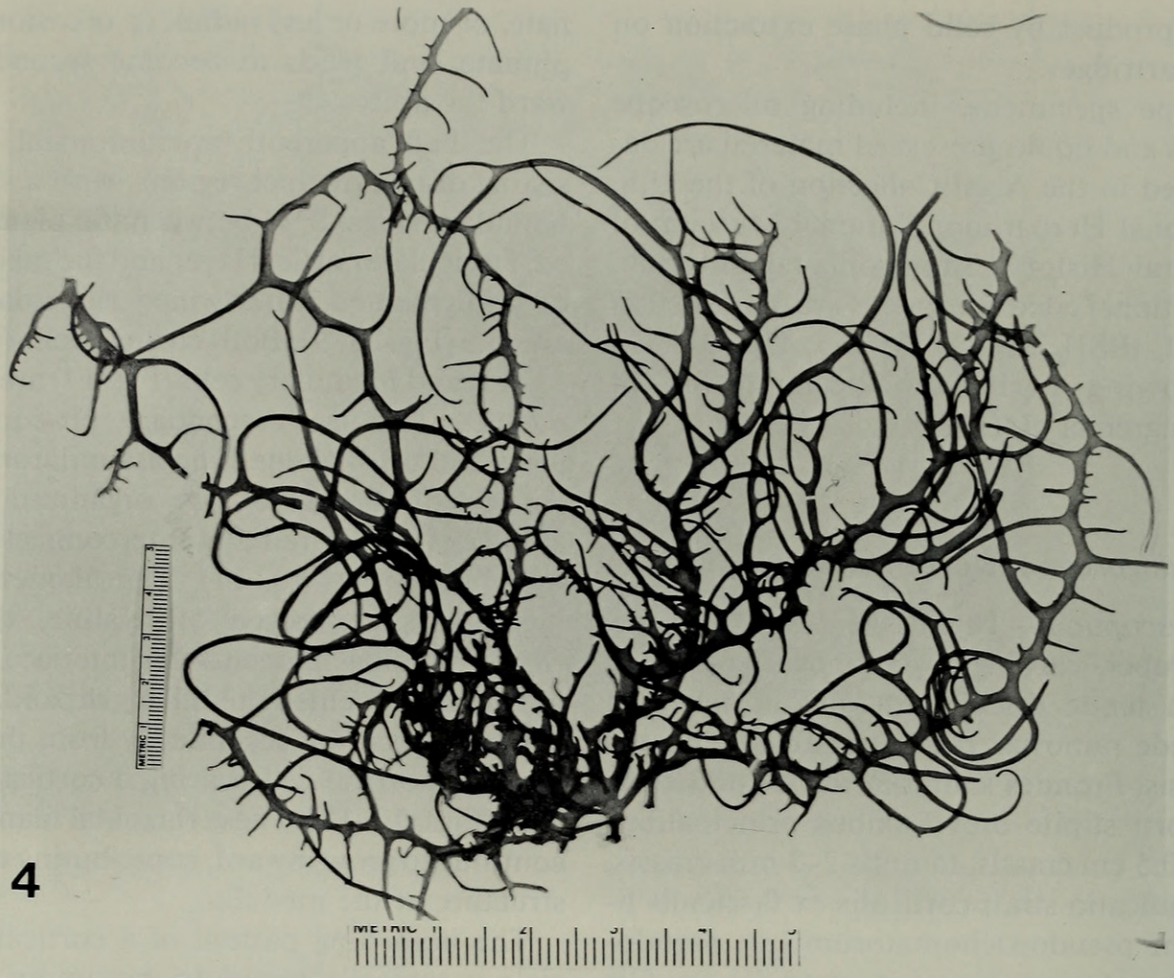
Rhodogorgon J. Norris et Bucher, gen. nov.

Description.—Thallus erectus rosealus vel atroruber, cartilaginogelatinosus, per hapteron tenue discoideum affixus, laxe vel abunde ramosus; ramis teretibus vel compressis. Frondes solitariae aut 2 aut 3 erectae orti stipite brevi; axibus principalibus 0.3–0.5 cm crassis, ramulis 2–3 mm crassis. Ramificatio strati corticalis ex fasciculis filorum pseudotrichomatorum aut pseudodichomatorum constans; medulla ex filis oblongatis eramosis rhizoidibus constans; rhizoidibus medullaris ab cellulis interioribus corticalibus ortis. Cellulae corticales et medullosae uninucleatae, conjunctionibus vegetativis et synapsibus secundis absentibus. Synapses primariae obturamentae cum duobus stratis capitularibus continentes, exterioribus tholiformibus. Extensio cellularum calcifera protoplasmica hyalina esegmentata cellulis interioribus fasciculorum corticalium orta, ad apicem cylindrica calcifera (calcite). Cellulae parentes spermatangiorum bilateraliter cellula subterminali filorum corticalium ortae, spermatangio singulo ferentes.

The thalli are erect, cartilaginous, slippery, locally lightly calcified, with terete to compressed upright main axes and side branches. Usually a single (rarely more) short stipe arises from a small, discoid holdfast. The thalli may be stringy and sparsely branched to a few orders, or compact and densely branched to several orders (Figs. 1–7). Branching is mostly irregular, or alternate, or more or less radial, or occasionally pinnate, and tends to become secund toward the apices.

The thalli apparently are multiaxial, consisting of two distinct regions, with a sharp boundary (Figs. 8, 9) between the pigmented, fasciculate cortical layer and the medulla of unpigmented, intertwined rhizoidal filaments (Figs. 8, 9). Both cortical cells (Figs. 11–13) and medullary cells (Fig. 17) are uninucleate and lack secondary pit-connections and cell fusions. The assimilatory filaments of the cortex are organized into fascicles that are radially interconnected at their base (Figs. 10, 11). The filamentous medulla is composed of hyaline, thick-walled rhizoidal filaments that interlace. One or two unpigmented medullary rhizoidal filaments are cut off secondarily from the innermost cortical cell bearing a cortical fascicle (Figs. 10–13). These rhizoidal filaments continue to grow inward, contributing to the structure of the medulla.

The branching pattern of a cortical fascicle is typically pseudotrichotomous, and there are three types of cortical structures. The first are filaments composed of pigmented, granular, cylindrical cells that terminate in an inflated hyaline cell (Figs. 16, 18, 21, 23–26). The second type are basal hair cells (Figs. 18–20), and the third are unique, elongate, unsegmented, hyaline, hair-like calciferous cells, which are distally surrounded by a brownish, "husk-like" calcareous structure (Figs. 21–26). A new branch within a cortical fascicle originates when a cell of a pigmented filament buds part of its cytoplasm distally (Figs. 13, 14). Subsequent septation of the protruded cytoplasm (Fig. 15) followed by cell division towards the thallus surface results in a new branch. The septum develops horizontally (Fig. 15) or slightly obliquely. The pseudotrichotomy of the cortical fascicle results when a cell that bears a pseudodichotomy buds (Fig. 13), septates, and undergoes cell division. Concordantly, a pseudodichotomy originates when the bearing cell of an unbranched cortical filament protrudes and



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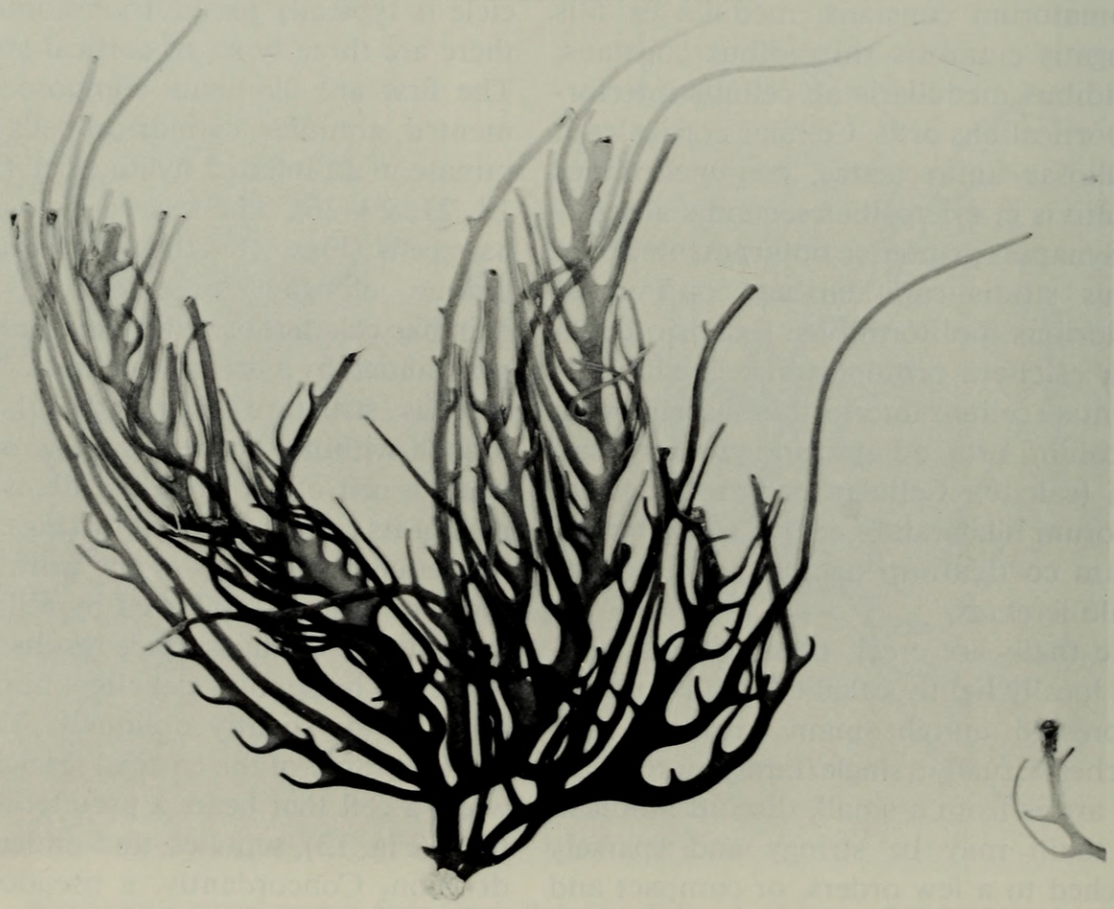

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divides (Figs. 14, 15). Well developed branches have a central branching point that has cut off rhizoids and bears two orders of trichotomies (Fig. 13). An unbranched cortical filament usually consists of 4–6 cells (Figs. 10, 11).

Cell division does not always produce a new side branch, but may stop after cutting off one cell that becomes the basal cell of a hair (Figs. 18, 19). Cytological transformation of such a basal cell is often accompanied by breakdown of its cell wall material, revealing persistent putative cellulose fibrils (Figs. 18, 19). Once the basal cell primordium becomes dense with cytoplasm and increases in size (Fig. 19), it cuts off a similarly darkly staining hair (Fig. 20) that protrudes beyond the cortical surface. If the hair is broken off, the pit-connection between the cells persists.

The specialized, brownish, "husk-like" structures of the calciferous cells are the localized sites of extracellular calcite precipitation. When dilute acid is pipetted underneath the coverslip, the calcite readily dissolves, revealing a hyaline, small to large, inflated tip on the elongate, unsegmented, hair-like cell. These hair-like cells are very thin, vacuolate protoplasmic extensions that are cut off and pit-connected to the base of a pseudotrichotomy (Figs. 24, 27) or pseudodichotomy (Fig. 26). The calcite completely surrounds the apical portion of the calciferous hair-like cell when it is narrow (Fig. 21), but as its tip inflates a longitudinal furrow (Figs. 22, 23) forms, and the narrow extension slightly expands in width (Figs. 24–26). Occasionally a very narrow channel forms within the cell wall of the hyaline, calciferous extension (Fig. 22). The calcite "husk-like" structures are scattered among and located just beneath the zone of the terminal inflated cells of the cortical filaments (Figs. 8, 9, 21, 23, 26). These unique calcite structures vary in abundance within the cortical layer and give a greyish sheen to the thallus. The calciferous cells are commonly one per fascicle, but up to three may be cut off. Segmentation within these calciferous cells was never observed, although their apical portions were occasionally separated from the remaining portion of the cell by a lenticular wall (Fig. 28).

Plants are apparently dioecious. In spermatangium bearing gametophytes, the cortex consists of a continuous zone of spermatangial parent cells (Fig. 29). Spermatangial parent cells are borne bilaterally on the subterminal cell of a cortical filament (Fig. 30), each cutting off a single spermatangium (Fig. 31) by oblique division.

Remarks.—*Rhodogorgon* is named for its resemblance to the branching soft corals, the gorgonians (Gorgonacea). *Rhodo-* means red and *-gorgon* refers to Gorgon, a figure in Greek mythology (Genaust 1976), and the other gorgons, Euryale, Steno and Medusa, who had hair of snakes.

Type species.—*Rhodogorgon carriebowensis.*

Key to the species of *Rhodogorgon*

1. Plants loose, sparingly branched to 2–3 orders, with determinate and indeterminate ultimate branches . . . . . *R. carriebowensis*
– Plants more compact, densely branched to 3–5 orders, with determinate ultimate branchlets . . . . . *R. ramosissima*

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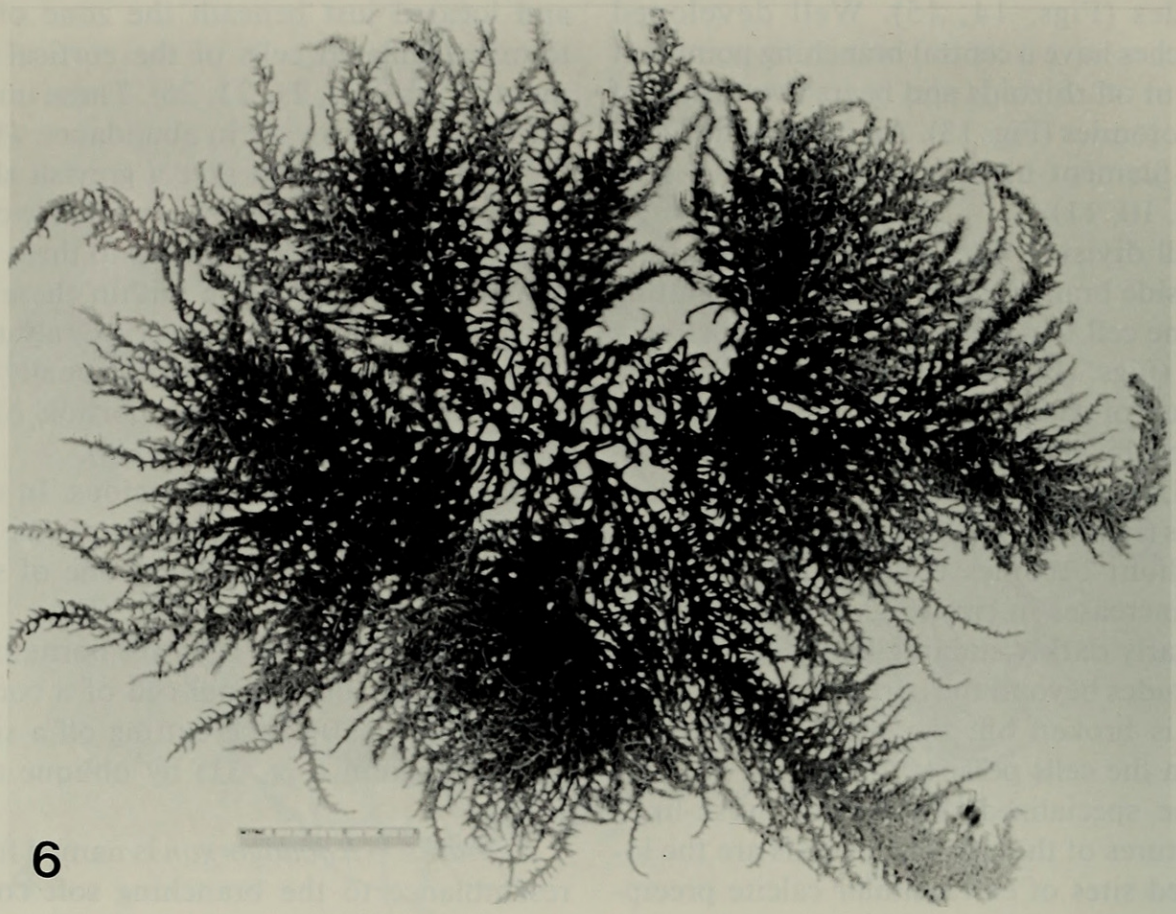
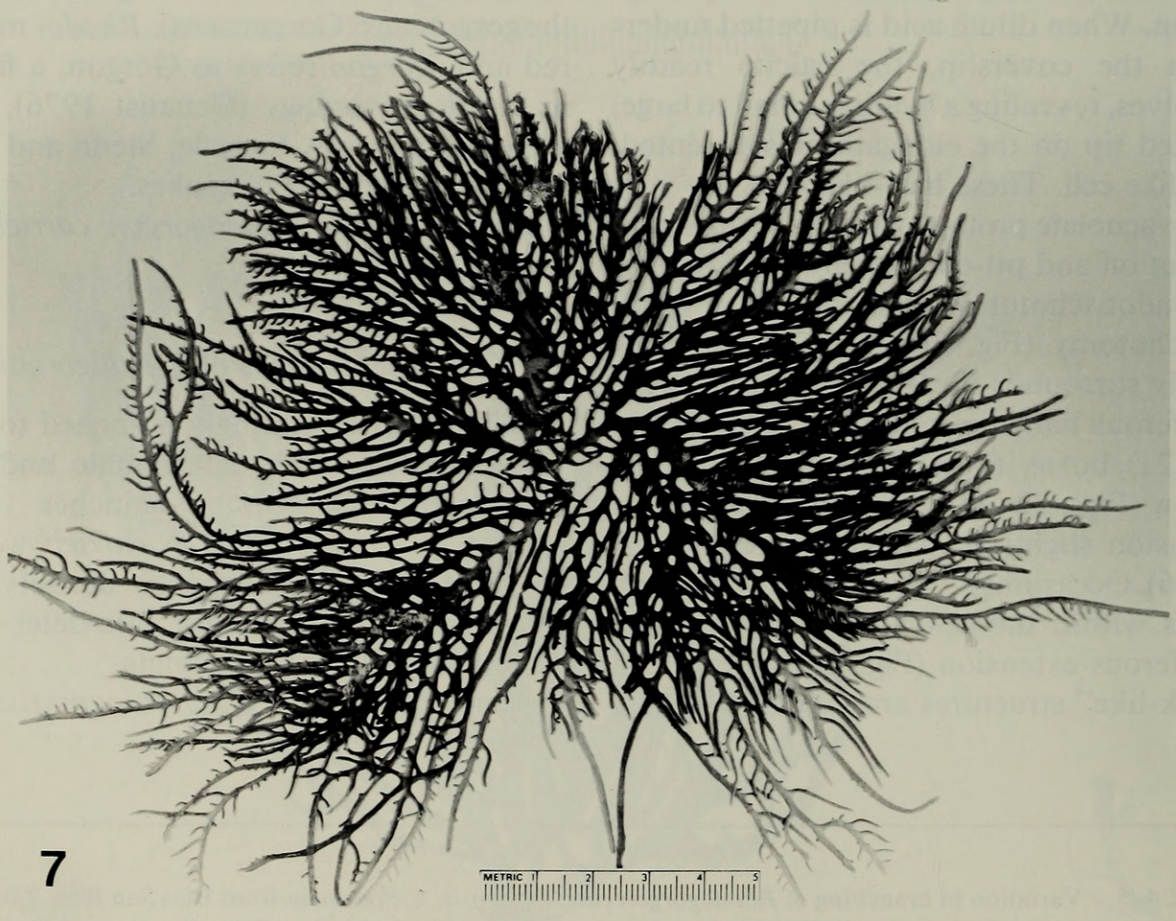
Figs. 4–5. Variation in branching of *Rhodogorgon carriebowensis.* 4, Specimen from Islas San Blas, Panama, with both long and short branches (US-098366). 5, Specimen from Passe du Marin, off Pte. Borgnesse, Martinique (US-098367).





Figs. 6–7. *Rhodogorgon ramosissima.* 6, Holotype from Carlisle Bay, Antigua (US-098361). 7, A more openly branched form, from Pte. Borgnesse, Martinique (US-098365).

Rhodogorgon carriebowensis
J. Norris et Bucher, sp. nov.
Figs. 1–5, 8–31

Diagnosis.—Thallus usque ad 50 cm, inferne atropurpureus, superne aurantio-rosealus. Frondes solitariae aut raro 2 aut 3, sparse vel profuse 1-2(-3)-plo ramosae; axibus ad 1.0 cm diam.; ramis saepe longis teretibus ad 6 mm diam. et 9.0–13.5(–40) cm longis; cellulis medullosis plusminusve 4.5 μm diam. et ad 90 μm longis; extensionibus calciferis 1–4 μm diam. et 40–65 μm longis, ad apicem calciferum 10 μm diam. et 25 μm longis.

The thalli are cartilaginous, slippery, to 50 cm tall, dark purple to light peach, usually darker below and lighter above, with a greyish tint throughout. A single (rarely two or three), short stipe grades into terete to compressed axes, to 1.0 cm diam. The axes branch irregularly, alternately, or occasionally more or less radially up to three orders. The branches are terete, short to long, to 6 mm diam. and up to 40 cm long (Fig. 2), with blunt ultimate branches to 4 mm diam.

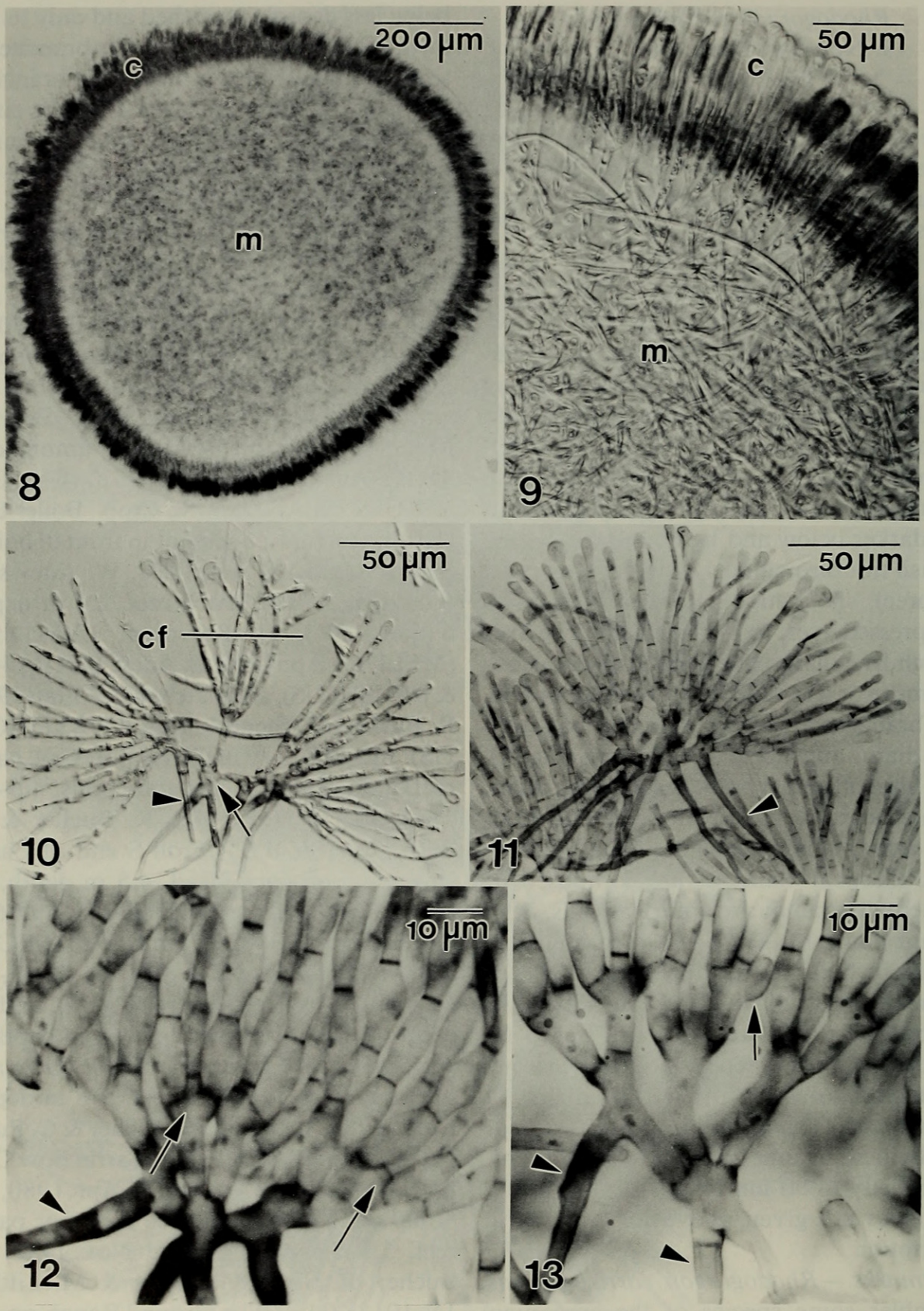
The cortex in cross section is 70–105 μm wide and distinctly separate from the medulla. Cortical filaments are composed of pigmented, granular, cylindrical cells, 1.5–6.0 μm diam. by 12–18 μm long, that terminate in bulbose, hyaline cells, 6–10 μm diam. by 9–14 μm long. The hyaline, calciferous cells are 1–4 μm diam. by 40–65 μm long, with a swollen tip, and bear unique, calcite structures distally, 10 μm diam. by 25 μm long. The medulla is composed of intertwined, hyaline, thin cells, 4 μm diam. and mostly to 90 μm long. All other characteristics are given above in the generic description.

Remarks.—*Rhodogorgon carriebowensis* resembles some species of the gorgonian *Carijoa.* It is named after Carrie Bow Cay, the type locality and site of the Smithsonian's Caribbean Coral Reef Ecosystem Program (CCRE) on the Belizean Barrier Reef. This species differs from *R. ramosissima* in being less densely branched and only to two or three orders, with the upper branches in some tending to be secund. The branches, including the ultimate branchlets, are either determinate or indeterminate, and sometimes are very long, to 40 cm. See *R. ramosissima* for other differences.

Type.—Carrie Bow Cay, Belizean Barrier Reef, Belize, spur and groove zone, 4.6–12.2 m depth, 1 May 1979, K. E. Bucher, JN-7520 (holotype: Alg. Coll. #US-098360).

Distribution.—Caribbean Sea: Bahamas, St. Croix, Belize, Martinique, Panama.

Paratypes.—Caribbean Sea: BAHAMAS.—Chub Cay, 4 m depth, among corals, 12 Jun 1989, R. Sims, s. n. (US). U.S. VIRGIN ISLANDS.—St. Croix: Boiler Bay, growing on fore-pavement in front of boiler, 3–4 m depth, 19 Aug 1978, W. Adey s. n. (US); Tague Bay, patch reef, 2.4 m depth, 6 Jan 1973, C. Bowman, IAA-11592 (MELU), 5 Apr 1973, P. Adey, IAA-11447a & b (BISH, US), and patch reef, 25 Jan 1974, R. Burke & R. Steneck, IAA-11783 (MICH, US). BELIZE.—W of Carrie Bow Cay, patch reef, among gorgonians and corals, 4.6–6.1 m depth, 25 Nov 1980, K. Bucher & R. Sims, JN-10670 (UC); off S end of Carrie Bow Cay, on coral head, 4.5 m depth, 30 Mar 1980, M. Hay, RHS-80-275, and 6 m depth, 9 Apr 1980, R. Sims, s. n. (MICH); SW of Carrie Bow Cay, 3.0 m depth, 25 Mar 1980, M. Hay, s. n. (UC, US), and on coral rubble, patch reef, 6.1–9.1 m depth, 1 Apr 1985, M. Littler, JN-12477 (US), and under coral head, patch reef, 5–8 m depth, 5 Apr 1989, J. Norris, K. Bucher & C. Pueschel, JN-16241 (US); SE of Carrie Bow Cay, patch reef, 4.6 m depth, 28 Apr 1980, R. Sims, s. n. (US); vic. of Wee Wee Cay, patch reef, 1.5–7.6 m depth, 25 Nov 1980, K. Bucher, R. Sims, P. Taylor & M. Littler, JN-10138 (US); Blue Ground Range, on *Acropora palmata,* 0.3–1.5 m depth, 10 Apr 1985, C. Tanner, JN-14830 (US). MARTINIQUE.—between Ilet au Chiens and Pte. Ferre, 8 m depth, 25 Aug 1985, K. Bucher & B. Brooks, KB-1687 (US); Pte. Borgnesse,



Figs. 8–13. Anatomy of *Rhodogorgon carriebowensis*. 8, Transverse section through a third order branch showing cortical cells (c) sharply demarcated from the medullary region (m) of intertwined rhizoidal filaments (unstained, Nomarski). 9, Close-up of Fig. 8 showing junction between cortex and medulla (unstained, Nomarski). 10–11, Assimilatory filaments organized into cortical fascicles (cf) radially interconnected at their base (arrow), and rhizoidal filaments (arrowhead) cut off from innermost cortical cell bearing fascicle (Nomarski). 12, Close-up of base of cortical fascicle, showing pseudotrichotomous branching (arrow), uninucleate cortical cells and

3.0–18.3 m depth, 23 Aug 1985, M. Hay, KB-1264 (US), to 12.2 m depth, 24 Aug 1985, M. Hay & L. Fisher, KB-1645 (US), and 5 m depth, 29 Aug 1985, M. Hay & K. Gustafson, KB-768 (US); Passe du Marin, off Pte. Borgnesse, 3.0–12.2 m depth, 28 Aug 1985, K. Bucher & B. Brooks, KB-1438 (ADU, MELU, UC, US), and 12 m depth, 28 Aug 1985, M. Hay & L. Fisher, KB-1447 (BISH, MICH, US). PANAMA.—Galeta Reef, N of STRI's Galeta Lab., 1 Jul 1978, M. Hay, MH-193 (US); San Blas Islands, SW side of Sail Rock, 6.1 m depth, 8 Aug 1979, J. Norris, s. n. (US).

Rhodogorgon ramosissima
J. Norris et Bucher, sp. nov.
Figs. 6–7

Diagnosis.—Thallus compactus ad 30 cm, obscure canescens vel atrovirens, plusminusve radialiter et profuse ad 5-plo ramosus; ramis distaliter tenuiorious ultimis brevis in diametro uniformibus. Cortex as 105 μm diam.; cellulis medullosis 3–4 μm latis et plerumque 140 μm longis; cylindricis calciferis plusminusve 27 μm longa et 12 μm diam.

The thalli of *R. ramosissima* are usually more compact and densely, more or less radially, branched to five orders, with the branches becoming progressively smaller outwards. The ultimate branchlets are short, of uniform diameter and have blunt apices. The color of *R. ramosissima* is generally darker, dark grey to blackish-green; the medulla and cortex are distinct, with the cortical layer to 105 μm wide; medullary cells 3–4 μm in diam. and mostly 110–150 μm long; the calcite structures of the calciferous cells are 12 μm diam. by 27 μm long.

Remarks.—This species differs from *R. carriebowensis* primarily in habit, being more densely branched, up to five orders. Branching tends to be radial, with the branches becoming progressively smaller and shorter outwards. The ultimate branches are short, apparently determinate, and of uniform diameter with blunt apices. The specific epiphet, *ramosissima,* is derived from *ramosus,* full of branches, and *-issimus* (adjectival superlative) meaning very or most. The air-dried herbarium specimens of *R. ramosissima* are similar to the gorgonian, *Plumigorgia.*

Type.—Carlisle Bay, Antigua, Lesser Antilles, on rocks, 0.5–6.1 m depth, 21 Aug 1985, K. E. Bucher & B. L. Brooks KB-1271a (holotype: Alg. Coll. US-098361; isotype: Alg. Coll. US-098362).

Distribution.—Caribbean Sea: Antigua and Martinique, Lesser Antilles.

Paratypes—Caribbean Sea: ANTIGUA.—Carlisle Bay, 0.5–6.0 m depth on rocks, 21 Aug 1985, K. Bucher & B. Brooks, KB-1271b (ADU, BISH, MELU, MICH); vic. Cade Reef, 10.7 m depth, 21 Aug 1985, K. Bucher, B. Brooks, & W. Fenical, KB-1551 (US). MARTINIQUE—near Petite Martinique in Havre du Robert, 1.5–3.0 m depth on rocks, 25 Aug 1985, W. Fenical, KB-1691 (MICH, UC, US); Pte. Borgnesse, 12.2 m depth, 24 Aug 1985, M. Hay & L. Fisher, KB-1647 (US); Ilet Rainville, 6.1 m depth, 26 Aug 1985, M. Hay, KB-699 (US).

Results.—The absorption spectrum peaks of the red algal phycobilisomes (Gantt 1981) of *R. carriebowensis* are 497 nm and 565 nm, indicating R-phycoerythrin as known only in the red algae. The fluorescence spectrum peak is 578 nm, indicating phycoerythrins as found in both red and blue-green algae. Comparative thin layer chromatographs revealed no apparent unusual secondary metabolites in the lipid extract. This suggests that *Rhodogorgon* is not chemically

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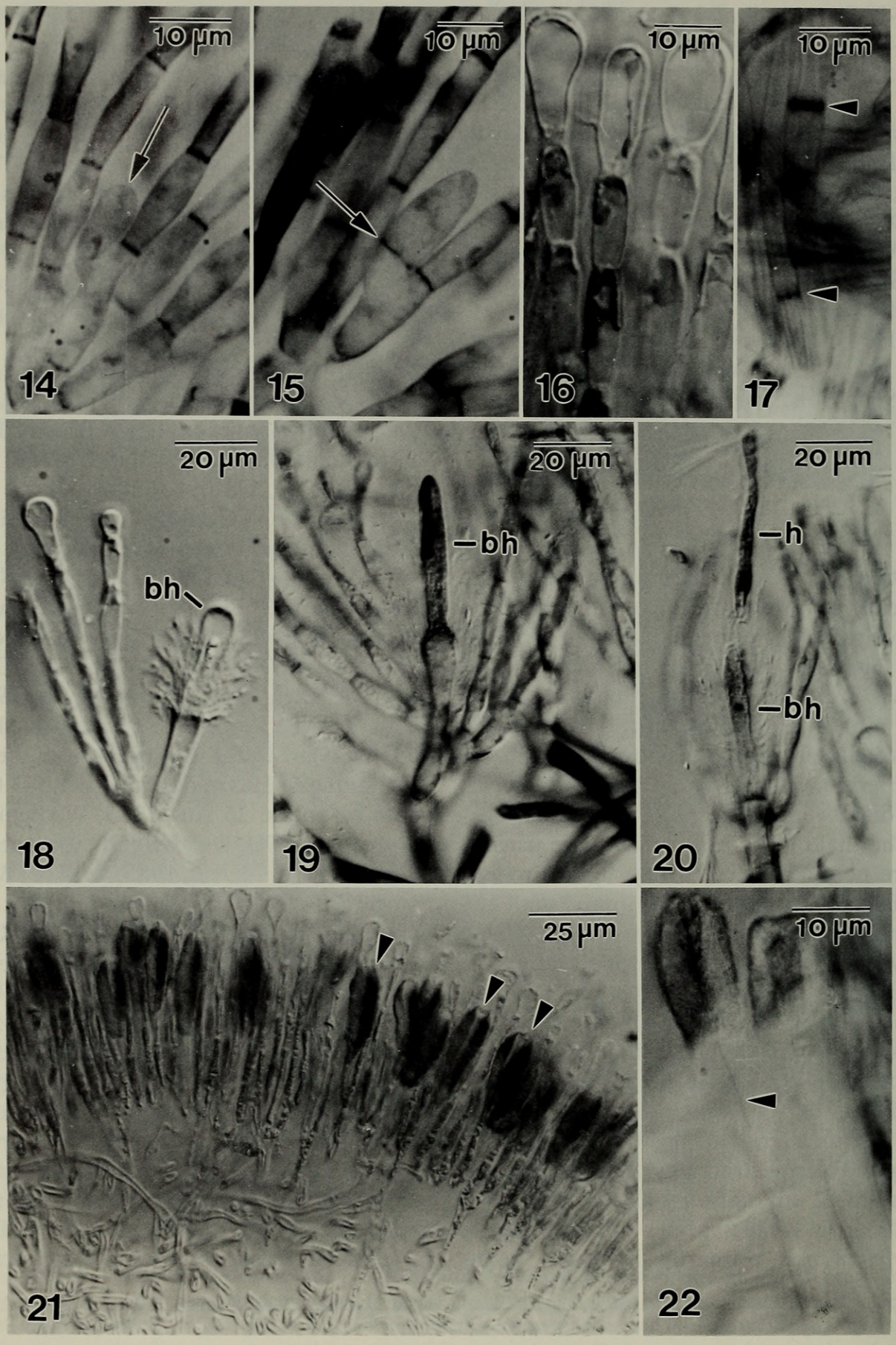
medullary rhizoidal filaments (arrowhead) (hematoxylin stained). 13, Cell within cortical filament budding off part of its cytoplasm distally (arrow) leading to pseudotrichotomy formation, and medullary rhizoidal filaments (arrowhead) cut off from base of cortical fascicle (hematoxylin stained).



Figs. 14–22. Anatomy of *Rhodogorgon carriebowensis*. 14, Cell within cortical filament budding off part of its cytoplasm distally (arrow) leading to pseudotrichotomy formation (hematoxylin stained). 15, Septation (arrow) of protruded cytoplasm leading to new filament is laid down horizontally (hematoxylin stained). 16, Thick-

defended (sensu Norris & Fenical 1982) against herbivory. Because of its resemblance to certain soft corals, we suggest it may elude predation as a gorgonian mimic.

Recently, hydroxy fatty acids chemically related to mammalian prostaglandins and leukotrienes have been isolated from the tropical red alga *Platysiphonia miniata* (Moghaddam et al. 1989). Studies on fresh homogenates of *R. carriebowensis* showed it apparently contains significant lipoxygenase activity resulting in the formation of a product with a UV absorbance spectrum indicative of conjucated diene. *Rhodogorgon* also appeared to contain measurable phospholipase A activity. The presence of these two enzymes suggests that *Rhodogorgon* may be capable of producing biologically active eicosanoid-like compounds (metabolites of arachidonic acid), thus far only known in these red algae.

The life history of *Rhodogorgon* is presently unknown. Because it is infrequently encountered and usually sparse where found, it may have a microscopic, filamentous or other hetermorphoric alternate not yet recognized. No tetrasporophytes of *Rhodogorgon* have been field collected, although they and its life history would likely have systematic implications.

Discussion.—A striking feature of *Rhodogorgon* is the presence of localized calcite deposits that envelop unsegmented, elongate, hair-like cells with inflated tips. These calciferous cells are cut off from the base of cortical fascicles and are not known to occur in any other alga. In the calcareous red algae, calcite is an unusual mineral form of calcium carbonate. The Corallinales (Silva & Johansen 1986) are the only other red algae known to precipitate calcium carbonate in this form; all other known calcified red algae possess aragonite (Borowitzka et al. 1974, Littler 1976). The Corallinales are considered to be an ancient group, having been found in limestone deposits from the late Cretaceous (Littler 1972), and extending as far back as the Jurassic (Johansen 1981). If calcite is the ancestral mode of calcium carbonate precipitation, perhaps *Rhodogorgon* is also a very old taxon.

The function of the calcite structures borne on the calciferous cells of the cortical fascicles is still unknown. Because the calcite is localized and only in the apical region, the cells may be involved in secondary branch formation and contribute to thallus structure. They could also play a role in nutrient boundary layer breakdown, or may be herbivore deterrents.

Ultrastructural features of pit-plugs have been useful in postulating phylogenetic affinites at ordinal levels (Pueschel & Cole 1982, Pueschel 1989). Presence of a dome-shaped outer cap layer on the pit plug is, besides *Rhodogorgon,* only reported in the Corallinales, Batrachospermales and some Acrochaetiales (Pueschel 1989). Since *Rhodogorgon* shares morphological characteristics with the former two orders, it will be briefly compared with them for possible taxonomic affinities. Although *Rhodogorgon* shares pit plug characteristics and calcite with the Corallinales, their vegetative and reproductive morphologies are very different. *Rhodogorgon* is unique among all the algae in the location and specialized structures of calcium carbonate deposits (for

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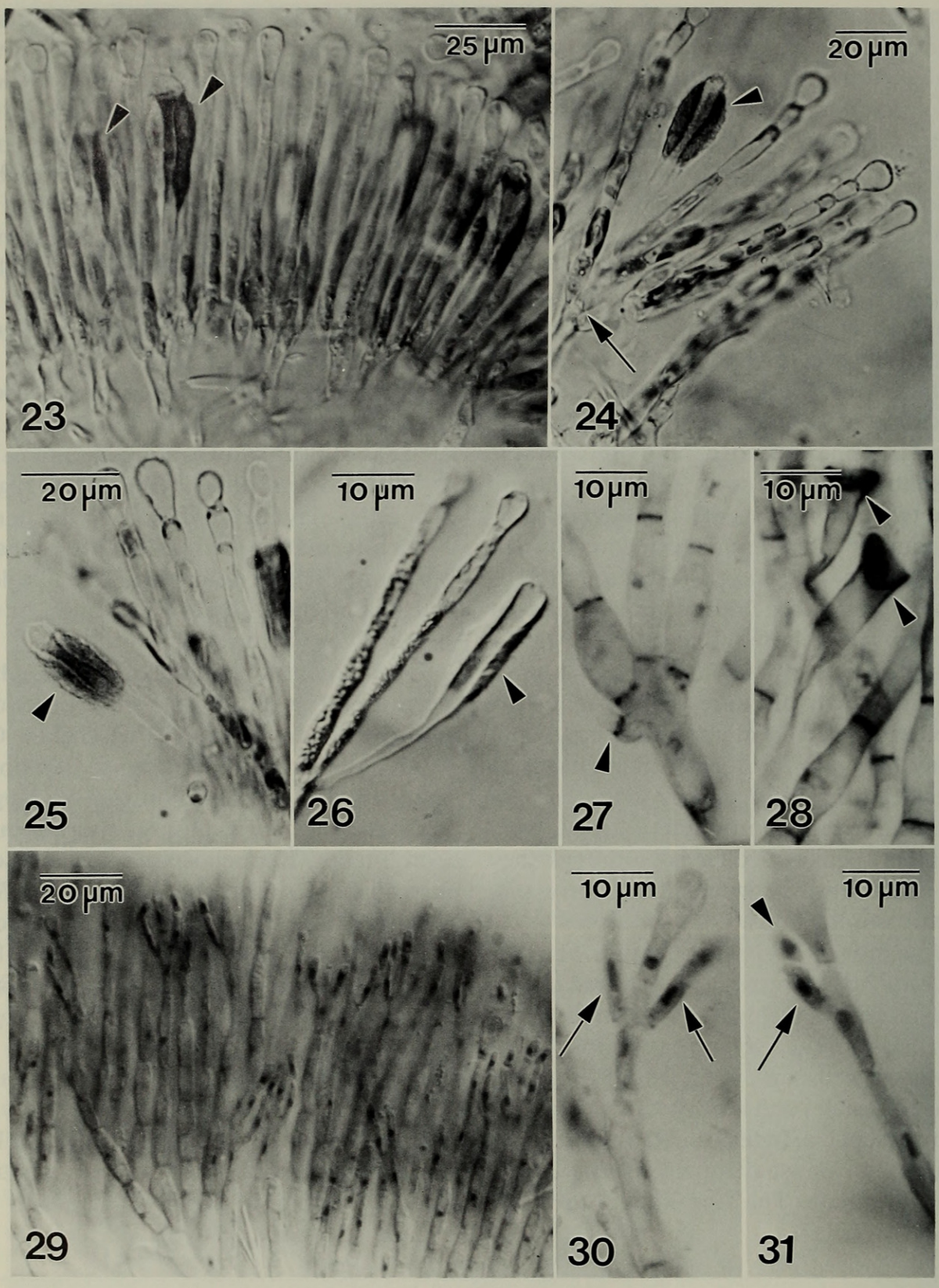
walled, vacuolate, inflated mature terminal cells of assimilatory filaments; chloroplasts of intercalary cortical cells are parietal (unstained, Nomarski). 17, Close-up of thick-walled, medullary rhizoidal filament showing pit-connection and pit ring (arrowhead) (hematoxylin stained). 18, Basal cell (bh) of hair erupting cellulose fibrils from cell wall (unstained, Nomarski). 19, Darkly stained basal cell (bh) that will develop a hair cell (hematoxylin stained, Nomarski). 20, Densely staining hair cell (h) pit-connected to its basal cell (bh) (hematoxylin stained, Nomarski). 21, Calcite surrounded apices (arrowheads) of elongate, calciferous cells embedded in cortex (unstained, Nomarski). 22, Narrow channel within wall of a calciferous cell (unstained).



Figs. 23–31. Anatomy of *Rhodogorgon carriebowensis*. 23, Hyaline, elongate, calciferous cells with calcite structures (arrowhead) located among the cortical filaments (unstained, Nomarski). 24, Elongate calciferous cell, bearing calcite structure (arrowhead), that is pit-connected (arrow) to base of pseudotrichotomy (unstained). 25, Formation of a longitudinal furrow within calcite covered apex (arrowhead), and emergence of inflated tip of a calciferous cell (unstained). 26, Calciferous cell at base of a pseudodichotomy, and partially dissolved calcite deposit (arrowhead) (unstained, Nomarski). 27, Pseudotrichotomy with basally pit-connected (arrowhead) remnant of a calciferous cell (hematoxylin stained). 28, Apical portion of a calciferous cell which is separated from

summary of calcification in the algae, see Littler & Littler 1984). The domoid expansion of the outer cap layer on the pit plug may be a primitive trait. If possession of a dome-shaped outer cap is ancestral, it may again indicate that *Rhodogorgon* is a very old taxon.

Among the Batrachospermales, *Rhodogorgon* is morphologically most similar to *Thorea* in the Thoreaceae, a family recently transferred from the Nemaliales to the Batrachospermales (Pueschel & Cole 1982). In contrast to the Thoreaceae, other members of the Batrachospermales are uniaxial and composed of axial filaments of indeterminate growth surrounded by whorled lateral filaments of limited growth (Aghajanian & Hommersand 1980). The Thoreaceae are multiaxial (Swale 1962, 1963; Yoshizaki 1986). In both *Rhodogorgon* and *Thorea* the basal cells of assimilatory branches produce rhizoidal filaments that contribute to the structure of the medulla. However, their cortical fascicles differ, being basically pseudotrichotomous in *Rhodogorgon* and pseudodichotomous in *Thorea.* Also, *Rhodogorgon* is marine and calcified, whereas the Thoreaceae are exclusively freshwater (Sheath 1984) and lack calcification. Interestingly, two different types of carposporophyte development have been described for two species currently placed in *Thorea.* In *T. bachmannii* Pujals ex Pujals from Brazil, Necchi (1987) illustrated a compact carposporophyte, whereas Yoshizaki (1986) observed a diffuse carposporophyte in *T. okadai* Yamada from Japan. These differences could indicate that the Thoreaceae may be polyphyletic, and that some members of the family (e.g., *T. okadai*) may be more closely related to some of the Nemaliales, such as *Dotyophycus* (Abbott & Yoshizaki 1981) and *Yamadaella* (Abbott 1970), and others, such as *T. bachmannii,* to the Batrachospermales. So far, only *T. riekei* Bischoff (1965) has been investigated for pit plug morphology, and if *T. okadai* lacks an outer dome pit plug cap, it would be more related to the Nemaliales. The systematic position of *Thorea* needs to be critically reinvestigated.

Rhodogorgon shares certain anatomical similarities with some members of the Galaxauraceae Parkinson and Liagoraceae Kützing of the Nemaliales. Although both families contain some calcareous members, they possess only aragonite (Borowitzka et al. 1974, Littler 1976, Okazaki et al. 1982). Apical depressions containing an apical cell that directs cell growth in members of Galaxauraceae were not seen in *Rhodogorgon,* but the presence of intertwined medullary filaments is reminiscent of *Galaxaura* and *Scinaia.* In the latter genera, basal cells of the cortical filaments cut off rhizoids and the process of cortex differentiation is mainly one of vacuolization accompanied by inflation in the terminal utricles (see Ramus 1969, for *Scinaia,* as '*Pseudogloiophloea*'). One could envision that appression of the utricles in the Galaxauraceae is a more advanced trait than the non-appressed terminal inflations of *Rhodogorgon.* There are also reproductive differences. The male reproductive structures are very simple in *Rhodogorgon,* while in some Galaxauraceae (i.e., *Galaxaura, Actinotrichia, Nothogenia*) the spermatangial parent cells are organized within specialized conceptacles (Svedelius 1939, 1943; Magruder 1984); the other gen-

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the remaining portion by a lenticular wall (arrowhead), observed after dissolution of the calcite (hematoxylin stained). 29, Cortex with spermatangial parent cells and spermatangia (hematoxylin stained, Nomarski). 30, Pair of spermatangial parent cells (arrows) borne bilaterally on subterminal cell of cortical filament (hematoxylin stained). 31, Spermatangium (arrowhead) cut off singly from a spermatangial parent cell (arrow) (hematoxylin stained).

era produce spermatangia at the thallus surface (e.g., Huisman 1986 for *Scinaia*). The spermatangial configuration of *Rhodogorgon* is certainly simpler than in the calcified members of the Galaxauraceae.

In the Nemaliaceae (Farlow) DeToni et Levi and the Liagoraceae, main axes and branches are of the multiaxial 'Springbrunnen-type' (Oltmanns 1922), and thus very different from the vegetative anatomy of *Rhodogorgon* which lacks a central core of axial medullary filaments. The origin of spermatangial parent cells in *Rhodogorgon* is nevertheless reminiscent of that of *Yamadaella* (Liagoraceae), where spermatangial parent cells are borne on subterminal cells of cortical filaments (Abbott 1970). Spermatangial parent cells in *Yamadaella* frequently cut off a short chain of spermatangia (Abbott 1970), whereas those of *Rhodogorgon* were only seen to cut off a single spermatangium. *Yamadaella* and *Rhodogorgon* both have inflated terminal cells on their assimilatory filaments.

Conclusions.—Based on vegetative and reproductive anatomy, our light-microscope studies suggest that *Rhodogorgon* exhibits similarities with some Thoreaceae, Galaxauraceae and Liagoraceae, whereas based on pit plug morphology, it shows relationships with *Thorea* and *Nemalionopsis* of the Thoreaceae (Pueschel & Cole 1982, Pueschel 1989). However, it differs in several characteristics from all of these families, and based on its combination of unusual characters, we are of the opinion that the new genus is only ancestrally related to the families mentioned above, or via convergence has evolved some similiar characteristics. *Rhodogorgon* is hypothesized to be a primitive red alga that may have originated before the families of the Nemaliales were present and diversified, and so we believe it would be better placed in a family of its own. However, this assessment must await more detailed studies on the development of the female reproductive system, life history, and ultrastructural characteristics.

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