A new species of *Dudresnaya* (Dumontiaceae, Rhodophyta) from the Canary Islands

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Abstract — A deep-water species of *Dudresnaya*, *D. multiramosa* Afonso-Carrillo, Sansón et Reves sp. nov., is described from the Canary Islands. Gametophytes are terete and radially branched up to six orders, young branches are annulate but become non-annulate at maturity, hexagonal crystals are lacking in axial cells, rhizoids reach 60 µm in diameter, inner cells of cortical fascicles are tri- to pentachotomously branched, and outer cortical cells are ellipsoid / moniliform. Spermatangia are borne singly or in pairs on terminal or subterminal cortical cells of monoecious gametophytes. Carpogonial and auxiliary-cell filaments lack a thick mucilage coat, vegetative laterals or rhizoids. Generative auxiliary cells are smaller and distinguishable by shape from adjacent cells of the auxiliary-cell filament prior to diploidization. Cystocarps consist of up to 12 rounded gonimolobes and are distinctly cleft around the auxiliary-cell filament. Tetrasporophytes are unknown. The new species is mainly distinguished by the cell shapes and pattern of branching of the cortical fascicles and by the multilobed cystocarps. It differs from all other *Dudresnaya* species by its autapomorphic characters. The western Atlantic D. bermudensis Setchell, D. georgiana Searles and D. puertoricensis Searles et Ballantine, the Hawaiian D. littleri Abbott and the eastern Pacific D. colombiana Taylor are postulated to be most closely related to D. multiramosa as these are the only other members to display moniliform cortical fascicles among the seventeen described species of the genus.

Canary Islands / Dudresnaya multiramosa / Dumontiaceae / marine algae / morphology / Rhodophyta / seaweed / taxonomy

Résumé – Une nouvelle espèce de *Dudresnaya* (Dumontiaceae, Rhodophyta) des îles Canaries. Une espèce de profondeur du genre Dudresnaya, D. multiramosa Afonso-Carrillo, Sansón et Reyes sp. nov, est décrite des îles Canaries. Les gamétophytes sont cylindriques et ramifiés radialement jusqu'à six niveaux de ramification, les jeunes rameaux sont annelés mais deviennent non annelés à maturité, les cristaux hexagonaux manquent dans les cellules axiales, les rhizoïdes atteignent jusqu'à 60 µm de diamètre, les fascicules corticaux sont tri- ou pentachotomiquement ramifiés et les cellules corticales externes sont ellipsoïdes / moniliformes. Les spermatocystes sont isolés ou disposés par paires sur les cellules corticales terminales ou subterminales des gamétophytes monoïques. Les rameaux carpogoniaux et les rameaux auxiliaires ne sont pas recouverts par un épais mucilage, ni par des rameaux latéraux végétatifs ou des rhizoïdes. Les cellules auxiliaires génératives sont plus petites et reconnaissables par la forme des cellules adjacentes du rameau auxiliaire avant la diploïdisation. Les cystocarpes ont jusqu'à 12 gonimolobes arrondis et sont distinctement clivés autour du rameau auxiliaire. Les tétrasporophytes sont inconnus. La nouvelle espèce est principalement reconnue à la forme des cellules et la ramification des fascicules corticaux et aux cystocarpes multilobés. Le D. multiramosa diffère des autres espèces de

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Dudresnaya par ses caractères autapomorphiques. Les espèces de l'Atlantique occidental D. bermudensis Setchell, D. georgiana Searles et D. puertoricensis Searles et Ballantine, l'espèce de Hawaï D. littleri Abbott et celle du Pacifique oriental D. colombiana Taylor seraient les plus voisines de D. multiramosa car ce sont les seules à montrer des fascicules corticaux moniliformes parmi les 17 espèces décrites du genre.

Macroalgues marines benthiques / Dudresnaya multiramosa / Dumontiaceae / îles Canaries / morphologie / Rhodophyta / taxinomie

INTRODUCTION

The genus *Dudresnaya* P.L. et H.M. Crouan (1835) is represented world-wide by seventeen species characterized by uniaxial, gelatinous, ephemeral spring-summer annual fronds with simple, spatially separated carpogonial and auxiliary-cell filaments (Tabares *et al.*, 1997, Abbott & McDermid, 2001). Robins & Kraft (1985) and Kajimura (1993, 1994) have constructed keys and tabular summaries of the specific boundaries of *Dudresnaya* that include most of the known species.

Three species of *Dudresnaya* have been reported from the Canary Islands: the endemic *Dudresnaya canariensis* Tabares, Afonso-Carrillo, Sansón et Reyes, the amphi-Atlantic *D. crassa* Howe, and the eastern Atlantic / Mediterranean type species of the genus, *D. verticillata* (Withering) Le Jolis (Afonso-Carrillo & Sansón, 1999). Recent studies carried out on the ephemeral spring-summer flora of deep-water cobble and bare-rock substrata in some areas of the Canary Islands have resulted in collection of a number of interesting species, including new records (Sansón *et al.*, 1991; Reyes *et al.*, 1993; Martín *et al.*, 1996), and species (Tabares *et al.*, 1997; Afonso-Carrillo *et al.*, 1998; O'Dwyer & Afonso-Carrillo, 2001). Material of a new species of *Dudresnaya* from these habitats in the island of Tenerife is described here.

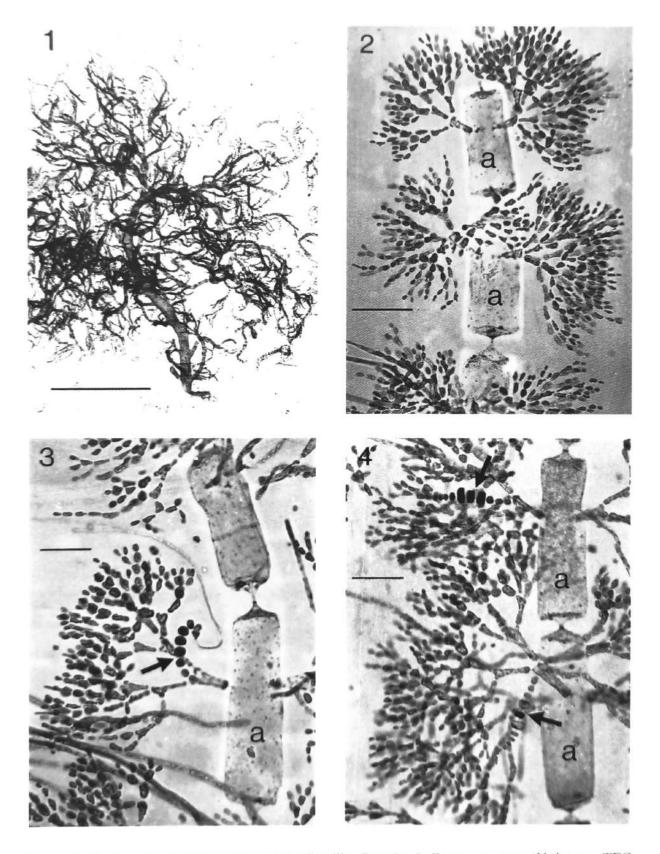
MATERIALS AND METHODS

A single liquid-preserved specimen was fixed in 4 % formalin in seawater. Selected fragments were stained in 1 % aniline blue, mounted in a 50 % Karo® corn syrup solution, and slightly squashed to separate the filaments. Drawings were obtained by using a camera lucida attached to a Zeiss microscope. Micrographs were taken on a Zeiss photomicroscope. Herbarium abbreviations follow Holmgren *et al.* (1990).

OBSERVATIONS

Dudresnaya multiramosa Afonso-Carrillo, Sansón et Reyes, sp. nov. (Figs 1-19)

Planta saxicolae, erectae usque 12 cm altae, lubricae cylindricae usque 3 mm diametro, radiatim irregulariter ramificati usque ad ordinem 6, ramis juvenibus annulatae. Cellulae axiales crystallis hexagonis carentes. Fila rhizoidealia usque



Figs 1-4. Dudresnaya multiramosa Afonso-Carrillo, Sansón & Reyes, sp. nov. (Holotype, TFC Phyc. 10230). Fig. 1. Habit of the holotype specimen. Scale bar = 30 mm. Fig. 2. Two successive axial cells (a) each bearing a whorl of cortical fascicles. Scale bar = 50 μ m. Fig. 3. Axial cell (a) bearing a cortical fascicle with a carpogonial filament (arrow). Scale bar = 50 μ m. Fig. 4. Axial cells (a) bearing cortical fascicles with auxiliary-cell filaments, the generative auxiliary cell (arrows) smaller than adjacent cells. Scale bar = 50 μ m.

60 µm diametro. Fasciculi corticales ramificati trichotome usque pentachotome; cellulae corticales magis externae ellipsoideae. Gametophyta monoica. 1-2 spermatangia super cellulis corticalibus terminalibus vel subterminalibus. Fila carpogonialia et fila cellulae auxiliaris tunica mucilaginosa crassa, filis lateralibus vegetativis et filis rizoideis carentia. Cellula auxiliaris generativa distinguibilis ante conjugationem cum filo conjunctivo. Cystocarpia multilobata usque 200 µm diametro et disjuncte fissa. Carposporangia ovoidea, 10-15 µm diametro. Tetrasporophyta ignota.

Plant saxicolous, erect, to 12 cm in height, lubricous; axes terete, to 3 mm in diameter, irregularly radially branched to six orders, with young branches annulate. Axial cells without hexagonal crystals. Rhizoidal filaments numerous, to 60 µm in diameter. Cortical fascicles trichotomously to pentachotomously branched; outer cortical cells ellipsoid. Gametophytes monoecious. Spermatangia single or in pairs on terminal or subterminal cortical cells. Carpogonial and auxiliary-cell filaments without a thick mucilage coat, vegetative laterals or rhizoids. Generative auxiliary cell distinct by shape and often size before fusion with connecting filament. Cystocarps multilobed, to 200 µm in diameter, distinctly cleft. Carposporangia ovoid, 10-15 µm in diameter. Tetrasporophytes unknown.

Holotype: TFC Phyc. 10230 (Fig. 1). 33 m depth, Playa de San Juan, Tenerife, Canary Islands, 14 September 1998; leg. J. F. González.

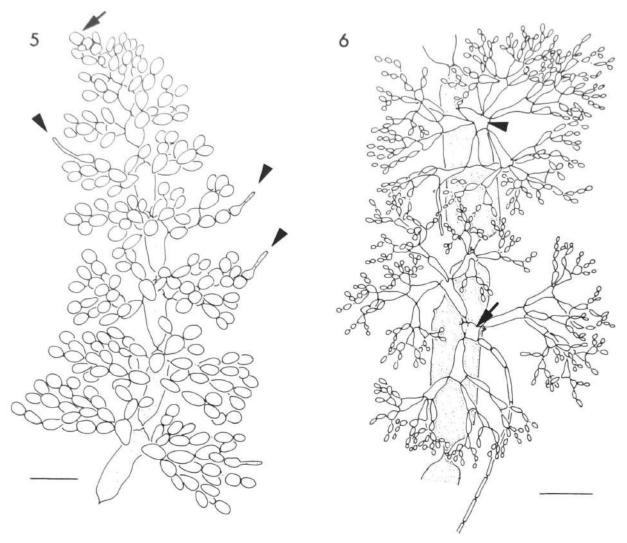
Etymology: The specific epithet refers to the abundant ramification of both the plant and cortical fascicles.

Distribution: Known only from the type locality and collection.

Habitat: The species grows on cobbles in a sand bed at 33 m depth along with *Lophocladia trichoclados* (C. Agardh) Schmitz, *Sporochnus pedunculatus* (Hudson) C. Agardh, *Dictyota fasciola* (Roth) Lamouroux and *Dictyopteris plagiogramma* (Montagne) Vickers.

Habit: Plant is erect, single from a discoid holdfast, up to 12 cm in height, light-pink in colour, gelatinous, lubricous, and irregularly radially branched up to six orders (Fig. 1). All axes are terete, the largest reaching 3 mm in diameter proximally and thinning to < 1 mm in diameter distally. Young branches are annulate and taper gradually to acute apices.

Vegetative structure: Indeterminate axes are percurrent and grow from apical cells 6 µm long and 4-6 µm in diameter (Fig. 5). Axial cells gradually increase in size, ranging from 120 µm in length by 50 µm in diameter in young branches < 500 µm in diameter to 1500 µm in length by 175 µm in width in branches > 2 mm in diameter. Hexagonal crystals are absent. Each axial cell produces a single whorl of 4-5 cortical fascicles along the distal third of its length, the fascicles progressively reaching a medial position as the axial cells elongate in mature axes (Figs 2, 5). The successive fascicles are initially distantly spaced, resulting in branches with an annulate appearance, but become confluent in mature branches. Cortical filaments (Fig. 2) are 6-10 cells long, relatively stiff, four to seven times branched at wide angles (> 60°), and up to 300 µm in length in young branches, reaching up to ca 1000 μm in length due primarily to elongation of the 1-4 basal cells, these accounting for up to 80 % of the fascicle length in mature axes. An indeterminate axis will occasionally and irregularly replace one of the determinate fascicles in a whorl, this in turn repeating the branching pattern of the main axes. Proximal branching of cortical fascicles is trichotomous to pentachotomous, with initially subcylindrical cells becoming progressively smaller, more moniliform and more regularly pseudodichotomous distally (Fig. 6). The basal 1-4 cells are up to 40 μ m in length by 10-12 μ m in width in branches < 0.5 mm in diameter, reaching 225 µm by 120 µm in older, thicker branches. Distal portions

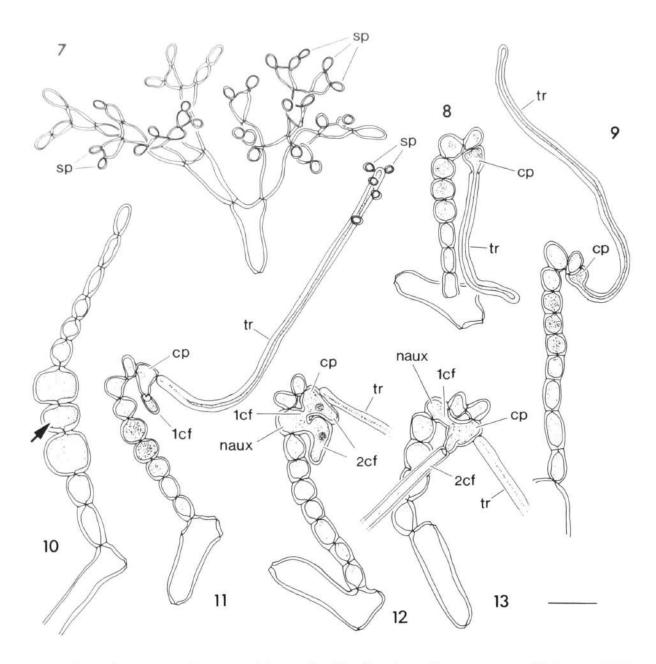


Figs 5-6. Dudresnaya multiramosa Afonso-Carrillo, Sansón et Reyes, sp. nov. (Holotype, TFC Phyc. 10230). Fig. 5. Uniaxial (arrow) apex and floridean hairs (arrowheads) borne terminally on some of the moniliform cortical fascicles. Scale bar = $20~\mu m$. Fig. 6. Portion of young branch showing axial cells and cortical fascicles, the basal and epibasal cells trichotomously (arrow) or pentachotomously (arrowhead) branched and the distal filaments pseudodichotomous. Scale bar = $20~\mu m$.

of fascicles are dichotomously (rarely trichotomously) branched (Fig. 6), the outer cortical cells being ellipsoid, 5-10 μ m in length by 3-5 μ m in width (Fig. 6); floridean hairs up to 30 μ m in length are common and concentrated towards the branch apices (Fig. 5).

Basal cells of cortical fascicles produce descending rhizoidal filaments (Fig. 6), which are simple or sparsely branched. They do not regularly give rise to secondary cortical laterals, although they occasionally grow into the cortex and branch distally, producing terminal cells 9-12 μ m in length by 2-3 μ m in diameter that are both longer and thinner than typical outer cortical cells. Rhizoids may sometimes increase from 10-20 μ m to 60 μ m in diameter in the thickest axes and can also arise from epibasal cells as well as the periaxial cells of the fascicles.

Reproduction: Gametophytes are monoecious, the spermatangial mother cells borne singly or in pairs on terminal and penultimate cortical cells (Fig. 7). Each mother cell produces one or two (rarely three) subspherical spermatangia 2.5-4 µm in diameter (Fig. 7).



Figs 7-13. Dudresnaya multiramosa Afonso-Carrillo, Sansón et Reyes, sp. nov. (Holotype, TFC Phyc. 10230). Scale bar = 20 μm. Fig. 7. Cortical filaments bearing spermatangia (sp). Figs 8, 9. Hooked carpogonial filaments terminated by mature carpogonia (cp). Fig. 10. Mature auxiliary-cell filament with generative auxiliary cell (arrow) located between two enlarged cells. Fig. 11. Carpogonial filament showing early postfertilization development of the carpogonium (cp), which is initiating a primary connecting filament (1cf). Note spermatia (sp) attached on the distal portion of trichogyne (tr). Figs 12, 13. Production of a secondary connecting filament (2cf) from the fusion complex formed by the carpogonium (cp), primary connecting filament (1cf) and nutritive auxiliary cell (naux).

Carpogonial and auxiliary-cell filaments are formed in place of vegetative filaments on the 1-3 innermost cells of cortical fascicles (Figs 3, 4), none being observed directly on axial cells in place of or in addition to the whorl elements. Carpogonial filaments are composed of 8-11 cells, six or seven of which are rounded and darkly staining whereas the two to four of the basal cells usually remain subcylindrical and lightly staining (Figs 3, 8, 9). After initiation of the

trichogyne, the carpogonium may undergo a single oblique or transverse division. The second cell below the carpogonium becomes wedge-shaped as a result of the unequal elongation of the cell and the apex of carpogonial filament becomes hooked (Figs 8, 9).

Auxiliary-cell filaments are composed of 10-15 cells (Figs 4, 10). The generative auxiliary cell is generally smaller and more flattened than adjacent cells, which become inflated and darkly stained, and occurs centrally in the filament (Figs 4, 10). Carpogonial and auxiliary-cell filaments never produce a thick mucilage coat neither vegetative laterals nor rhizoids on proximal cells.

Spermatia have been observed attached to the distal portions of trichogynes (Fig. 11), the carpogonium forming a primary connecting filament after presumed fertilization that fuses with the third and/or fourth cells (nutritive auxiliary cells) below the carpogonium (Figs 11, 12). Up to three secondary connecting filaments are formed from this fusion site (Fig. 13), these branching and the apices of the branches fusing laterally with a generative auxiliary cell (Fig. 14), after which the filaments collapse just behind their point of fusion. The portion of the connecting filament that remains attached to the auxiliary cell inflates somewhat and issues one or two ongrowing connecting filaments (Fig. 15) plus 3-5 pyriform gonimoblast initials (Fig. 16). The gonimoblast initials do not recurve around the generative auxiliary cell but divide distally to form 1-3 gonimolobe initials that develop synchronously into subpeltate gonimolobes (Figs 17, 18). Mature cystocarps are irregularly rounded, up to 200 µm in diameter, and consist of up to 12 discrete (rarely obscure) gonimolobes of fairly compactly arranged ovoid or angular carposporangia 10-15 µm in diameter (Fig. 19). The gonimolobes only rarely encircle the auxiliary-cell filament completely, a narrow slit that runs parallel to the auxiliary-cell filament normally being left along one side of the carposporophyte (Fig. 19). All cells of the auxiliary-cell filament become slightly enlarged during cystocarp formation, and occasionally the filament itself lengthens by the branched extension of 2-3 unmodified cells. Lateral filaments, however, are never formed on the proximal cells of the auxiliary-cell filaments.

Tetrasporophytes are unknown.

DISCUSSION

The new species is mainly distinguished by the shape and branching pattern of the cortical fascicles and by the morphology of the cystocarps. In regard to both features, *Dudresnaya multiramosa* exhibits characters apparently unreported in any other *Dudresnaya* species. Branching of cortical fascicles in other members of the genus is reported to be lateral, opposite, dichotomous or trichotomous (Eiseman & Norris, 1981; Searles, 1983; Robins & Kraft, 1985; Searles & Ballantine, 1986; Tabares *et al.*, 1997) but never until now tetra- or pentachotomous. Although Robins & Kraft (1985) did not include the pattern of branching of cortical fascicles among the characters used to separate *Dudresnaya* species, Tabares *et al.* (1997) showed that this feature can be reliably applied when making taxonomic distinctions within the genus.

In previous studies of *Dudresnaya* (Robins & Kraft, 1985; Kajimura, 1993, 1994; Tabares *et al.*, 1997) the morphology of mature cystocarps has been characterized on the basis of shape (globose, subglobose or reniform), the degree of compactness (loose or dense) of the carposporangia, or the degree to which the

Tab. 1. Comparison of Dudresnaya multiramosa Afonso-Carrillo, Sansón et Reyes, sp. nov. and related species.

Character	D. bermudensis ¹	D. colombiana ²	D. georgiana ³	D. liuleri ⁴	D. puertoricensis ⁵	D. multiramosa
Distribution	Western Atlantic (Bermudas, Bahamas, Florida)	Eastern Pacific (California, Gulf of California, Colombia	Western Atlantic (Georgia)	Central Pacific (Hawaii)	Western Atlantic (Georgia, Puerto Rico, Mexico)	Eastern Atlantic (Canary Islands)
Max. height of habit (mm)	06	50	40	75	80	120
Major branches	terete or compressed	terete or compressed	terete and villose	terete	terete	terete
Max. diameter of branches (mm)	no data	6.0	1.6	1.0	1.8	3.0
Annulations	absent	absent	absent	absent	present	present
Hexagonal crystals	no data	no data	absent	absent	present	absent
Hairs	no data	absent	present	absent / present	present	present
Shape of outer cortical cell	obovoid and moniliform	ellipsoid	ellipsoid to cylindrical	ovoid to spherical	ellipsoid	ellipsoid
Branching of inner portions of cortical fascicles	dichotomous	opposite or dichotomous	dichotomous to lateral	dichotomous	dichotomous to lateral	trichotomous to pentachotomous
Max. diameter of rhizoids (μm)	no data	=	9	15	18	09
Arrangement of spermatangia in cortical fascicles	terminal	terminal	lateral and scattered	terminal or subterminal	terminal or subterminal	terminal or subterminal

Tab. 1. (continued)

Character	D. bermudensis 1	D. colombiana ²	D. georgiana ³	D. littleri ⁴	D. puertoricensis ⁵	D. multiramosa
Carpogonial filaments bearing sterile laterals	no data	absent	present	present	present	absent
Auxiliary cell distinctly smaller than adjacent cells	present	absent	absent	absent	absent	present
Auxiliary-cell filaments bearing sterile laterals	present	absent	present	present	present	absent
Gonimoblast initiation	no data	auxiliary cell	connecting filament	connecting filament	connecting filament	connecting filament
Shape of cystocarp	reniform	no data	subglopose	subglobose	sabglobose	irregularly rounded and multilobed
Cystocarp distinctive cleft	no data	no data	present	present	no data	present
Max. diameter of cystocarps (μm)	126	180	120	430	140	200
Diameter of carposporangia (μm)	no data	5-10	8-9	15-25	6-5	10-15
Gametophyte	monoecious	dioecious	monoecious	dioecious	monoecious	monoecious

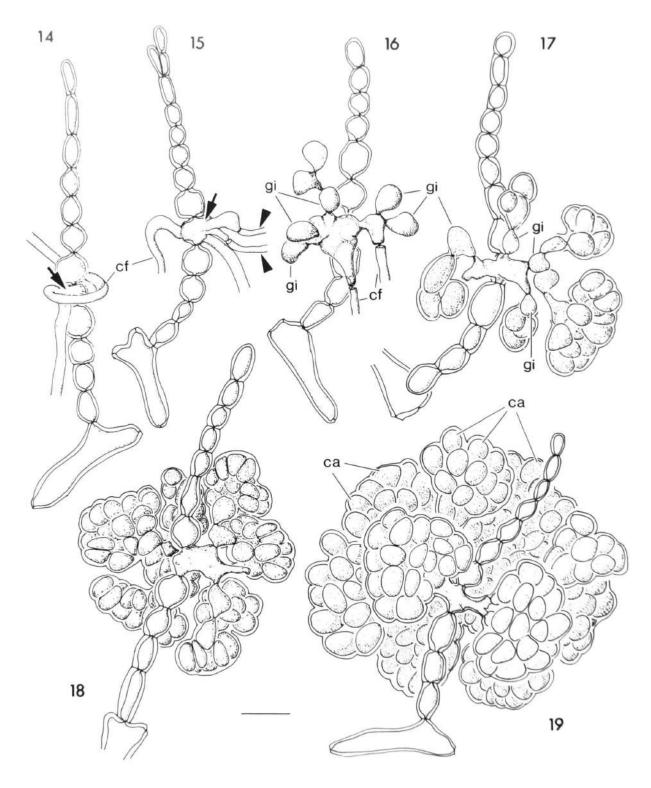
Data on D. bermudensis Setchell from Setchell (1912) and Taylor (1950, 1960).

² Data on D. colombiana Taylor from Taylor (1945), Mower & Widdowson (1969), Abbott & Hollenberg (1976) and Norris & Bucher (1976).

³ Data on D. georgiana Searles from Searles (1983), Schneider & Searles (1991) and Kajimura (1993).

⁴ Data on D. littleri Abbott from Abbott (1996, 1999), Abbott & McDermid (2001) and Littler (1974, as D. lubrica).

⁵ Data on D. puertoricensis Searles et Ballantine from Searles & Ballantine (1986) and Schneider & Searles (1991).



Figs 14-19. Dudresnaya multiramosa Afonso-Carrillo, Sansón et Reyes, sp. nov. (Holotype, TFC Phyc. 10230). Scale bar = 20 μm. Fig. 14. Generative auxiliary-cell (arrow) after fusion with a connecting filament (cf). Fig. 15. Two additional connecting filaments (arrowheads) arising from the swollen part of a connecting filament near its point of fusion with a generative auxiliary cell (arrow). Fig. 16. Five gonimoblast initials (gi) arising from the swollen fused portion of the connecting filament. Figs 17, 18. Early development of gonimoblasts, with relatively synchronous development of gonimolobes. Fig. 19. A multilobed mature cystocarp showing carposporangia (ca) arranged in discrete gonimolobes with the auxiliary-cell filament apparent through the cleft between gonimolobes.

gonimoblast completely or incompletely surrounds the auxiliary-cell filament. Only Womersley (1994) has called attention to the initially two-lobed cystocarps in *D. australis* J. Agardh *et* Setchell, other authors indicating but a single synchronously developing gonimolobe from the inception of gonimoblast growth in their morphological studies. Although other genera of the Dumontiaceae, as the multi-axial *Gibsmithia* Doty, produce cystocarps consisting of radiating gonimolobes (Kraft 1986), mature cystocarps composed of large numbers of discrete gonimolobes have not previously been reported for species of *Dudresnaya*. The morphology of cystocarps exhibited by *D. multiramosa* is therefore unique among the known species of the genus.

Dudresnaya multiramosa seems most closely related to D. bermudensis Setchell (1912), D. colombiana Taylor (1945), D. georgiana Searles (1983), D. littleri Abbott (1996) and D. puertoricensis Searles et Ballantine (1986), the only other species out of the seventeen species credited to the genus that have non-cylindrical cells in the outer cortex (Tab. 1). Of these, Dudresnaya bermudensis differs by its compressed branches, lack of annulations, more uniformly moniliform outer cortical cells, sterile laterals on lower cells of auxiliary-cell filaments, and smaller cystocarps (Setchell, 1912; Taylor, 1950, 1960). Dudresnaya colombiana differs by its compressed branches, lack of annulations, slender rhizoids (< 11 µm vs up to 60 µm), auxiliary cell that is indistinguishable from adjacent cells prior contact with connecting filaments, and gonimoblast that arise directly from the auxiliary cell rather than on the lateral protrusion formed at the site of connecting-filament fusion (Taylor, 1945; Mower & Widdowson, 1969; Abbott & Hollenberg, 1976; Norris & Bucher, 1976). Dudresnaya georgiana has villose branches, lacks annulations, produces slender rhizoids (< 6 µm), carpogonial and auxiliary-cell filaments that bear vegetative laterals, pre-diploidized auxiliary cells that are indistinguishable from adjacent cells, and smaller cystocarps and carposporangia (Searles, 1983; Schneider & Searles, 1991). Dudresnaya littleri differs by its slender rhizoids (< 15 μm), carpogonial and auxiliary-cell filaments that bear vegetative laterals, auxiliary cells that are indistinguishable from adjacent cells prior to diploidization, and larger cystocarps and carposporangia (Abbott, 1996; Abbott & McDermid, 2001; Littler, 1974, as D. lubrica). Dudresnaya puertoricensis has hexagonal crystals in the axial cells, slender rhizoids (< 18 µm), carpogonial and auxiliary-cell filaments that bear vegetative laterals, auxiliary cells that are indistinguishable before contact with a connecting filament, and smaller cystocarps and carposporangia (Searles & Ballantine, 1986; Schneider & Searles, 1991).

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