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Dudresnaya abbottiae sp. nov. (Dumontiaceae), a new gelatinous ephemeral spring-annual red alga from the Canary Islands

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Abstract — The marine red alga *Dudresnaya abbottiae* Afonso-Carrillo *et* Tabares sp. nov. from the Canary Islands is described. The new species has no single unique feature, but differs from the other *Dudresnaya* species by a distinctive combination of attributes. Gametophytes are radially branched with terete, nonannulate young branches, crystalline inclusions are lacking in axial cells, outer cortical cells are cylindrical, and rhizoidal filaments cut off from proximal cells of the cortical filaments reach 20 µm in diameter, regularly giving rise to terminal adventitious cortical fascicles. Spermatangial mother cells occur in paniculate clusters on outer cortical cells. Carpogonial and auxiliary-cell filaments lack a thick mucilage coat, generative auxiliary cells are distinguishable from adjacent cells before contact with a connecting filament, cystocarps are loosely constructed, and carposporangia completely surround the auxiliary-cell filament. The most closely related species to *Dudresnaya abbottiae* appear to be *D. babbittiana* Abbott *et* McDermid from the North Central Pacific, *D. capricornica* Robins *et* Kraft from Australia and the Arabian Sea, *D. kuroshioensis* Kajimura from Japan and *D. canariensis* Tabares, Afonso-Carrillo, Sansón *et* Reyes from the Canary Islands. Although all these species show important similarities in overall habit and shape of outer cortical cells, the arrangement of spermatangial mother cells and the morphology of rhizoids, generative auxiliary cells and cystocarps distinguish them. A synoptic key to the nineteen species currently included in the genus *Dudresnaya* is given.

Canary Islands / *Dudresnaya abbottiae* / Dumontiaceae / marine algae / morphology / Rhodophyta / seaweed / taxonomy

Résumé — *Dudresnaya abbottiae* sp. nov. (Dumontiaceae) une nouvelle algue rouge gélatineuse éphémère printanier des îles Canaries. L'algue rouge marine *Dudresnaya abbottiae* Afonso-Carrillo *et* Tabares sp. nov. est décrite des îles Canaries. La nouvelle espèce n'a aucun caractère unique, mais diffère des autres espèces de *Dudresnaya* par une combinaison distinctive de caractères. Les gamétophytes sont ramifiés radialement avec les jeunes rameaux de section circulaire, non annelés, les cristaux hexagonaux manquent dans les cellules axiales, les cellules corticales externes sont cylindriques et les rhizoïdes issus des cellules proximales des filaments corticaux, atteignent jusqu'à 20 µm de diamètre, donnant régulièrement naissance à des fascicules corticaux adventices terminaux. Les cellules mères des spermatocystes se produisent dans faisceaux paniculés sur les cellules corticales externes. Les rameaux carpogoniaux et les rameaux auxiliaires ne sont pas couverts par un épais

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mucilage, les cellules auxiliaires génératives sont reconnaissables des cellules adjacentes avant leur contact avec un filament de jonction, les cystocarpes sont lâchement construits et les carposporocystes entourent complètement le rameau auxiliaire. Il apparaît que les espèces les plus voisines de *Dudresnaya abbottiae* sont *D. babbittiana* Abbott *et* McDermid du Pacifique nord central, *D. capricornica* Robins *et* Kraft d'Australie et de la Mer de l'Arabie, *D. kuroshioensis* Kajimura du Japon et *D. canariensis* Tabares, Afonso-Carrillo, Sansón *et* Reyes des îles Canaries. Bien que toutes ces espèces montrent des similitudes importantes quant à l'aspect général et la forme des cellules corticales externes, elles peuvent être distinguées par la disposition des cellules mères des spermatocystes et la morphologie des rhizoïdes, les cellules auxiliaires génératives et les cystocarpes. Une clef synoptique des dix-neuf espèces actuellement placées dans le genre *Dudresnaya* est présentée.

algues marines / *Dudresnaya abbottiae* / Dumontiaceae / Iles Canaries / morphologie / Rhodophyta / taxinomie

INTRODUCTION

Recent studies carried out on sublittoral cobble and bare-rock substrata of the Canary Islands (Afonso-Carrillo *et al*., 2002) have allowed the recognition of a rich and diverse ephemeral spring-summer flora that, until the present, had remained overlooked. Species identified in these habitats are mainly red algae with soft and mucilaginous erect habits belonging to the uniaxial genera *Acrosymphyton* Sjöstedt, *Dudresnaya* P.L. *et* H.M. Crouan, and *Thuretella* Schmitz (Tabares *et al*., 1997; Tabares & Afonso-Carrillo, 1997; Afonso-Carrillo *et al*., 2002), and the multiaxial genera *Ganonema* Fan *et* Wang, *Helminthocladia* J. Agardh, and *Predaea* De Toni (Sansón *et al*., 1991; González-Ruiz *et al*., 1995; Afonso-Carrillo *et al.,* 1998; O'Dwyer & Afonso-Carrillo, 2001). The present account includes the description of a new ephemeral spring annual species of *Dudresnaya*, collected from shallow sublittoral habitats of the Canary Islands.

The genus *Dudresnaya* was established by P.L. & H.M. Crouan (1835) and includes uniaxial gelatinous algae with simple carpogonial and auxiliary-cell filaments that are morphologically distinct and spatially separated (Robins & Kraft, 1985). Species of *Dudresnaya* are defined primarily by a combination of vegetative and reproductive features that were listed by Robins & Kraft (1985) and Tabares *et al*. (1997), and most of the eighteen species currently recognized have very restricted distributions throughout warm seas (Littler, 1974; Searles, 1983; Searles & Ballantine, 1986; Kajimura, 1993, 1994; Afonso-Carrillo *et al*., 2002).

Eight *Dudresnaya* species are known in the Atlantic Ocean: *D. bermudensis* Setchell, *D. georgiana* Searles, *D. patula* Eiseman *et* J. Norris and *D. puertoricensis* Searles *et* Ballantine from few localities from the western Atlantic (Setchell, 1912; Searles, 1983; Eiseman & Norris, 1981; Searles & Ballantine, 1986); *D. canariensis* Tabares, Afonso-Carrillo, Sansón *et* Reyes, *D. multiramosa* Afonso-Carrillo, Sansón *et* Reyes, and the type species *D. verticillata* (Withering) Le Jolis are known only from the eastern Atlantic (Irvine, 1983; Tabares *et al*., 1997; Afonso-Carrillo *et al*., 2002); *D. crassa* Howe is the only species with an amphi-Atlantic distribution (Schneider & Searles, 1991; Afonso-Carrillo & Sansón, 1999). All four known species in the eastern Atlantic have been reported from the

Canary Islands, of which *D. canariensis* and *D. multiramosa* are endemic of these islands. *Dudresnaya abbottiae* sp. nov. is now added as the third endemic species of the genus in the Canary Islands.

MATERIALS AND METHODS

Liquid-preserved specimens were 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 made using a camera lucida attached to a Zeiss Standard microscope. Micrographs were taken on a Zeiss photomicroscope. Herbarium abbreviations follow Holmgren *et al*. (1990).

OBSERVATIONS

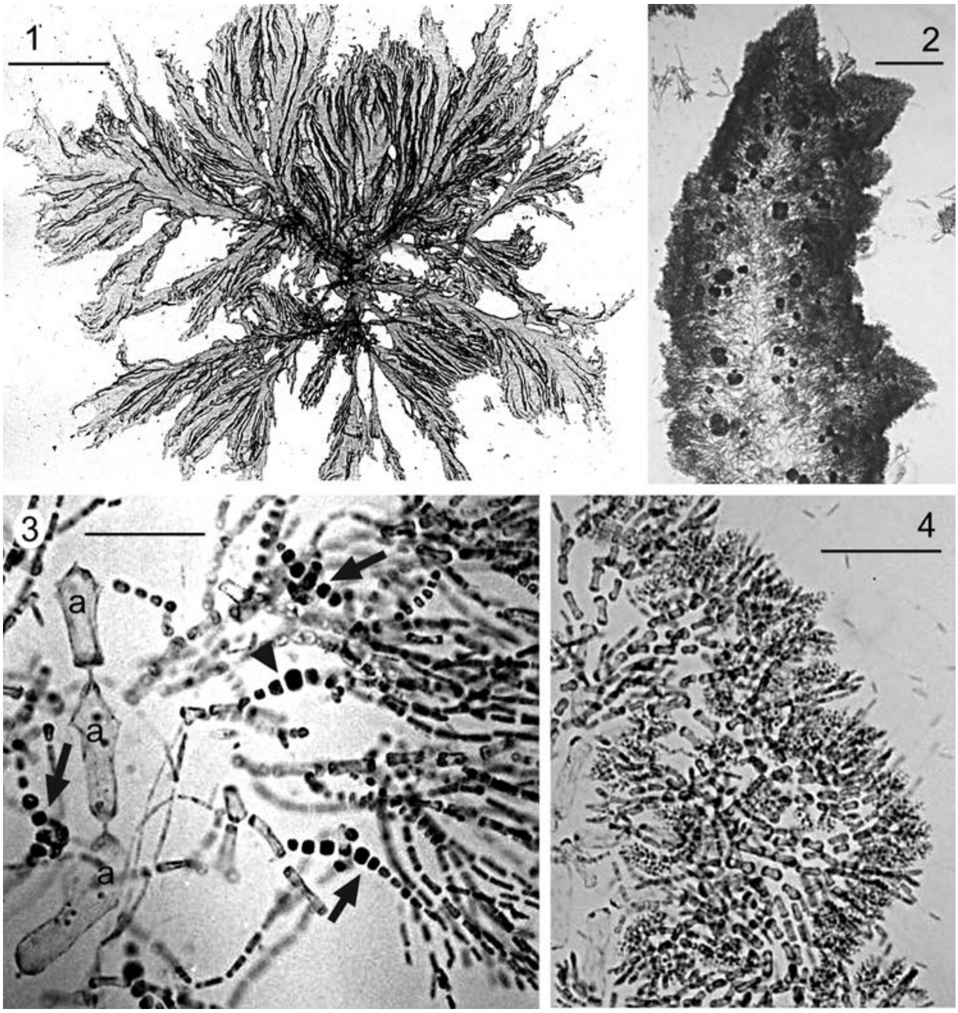
Dudresnaya abbottiae **Afonso-Carrillo** ***et*** **Tabares, sp. nov. (Figs 1-27)**

Plantae saxicolae, erectae usque 13 cm altae, axes gelatinosi, cylindrici usque 5 mm diametro, radiatim irregulariter ramificati usque ad ordines 5, sine annulis. Cellulae axiales crystallis carentes. Fila rhizoidealia usque 20 mm diametro, fasciculi corticales adventiciis terminalibus producentia. Fasciculi corticales flexuosi ramificati subalterne et dichotome; cellulae corticales magis externae cylindricae. Gametophyta dioica. Spermatangia racemos paniculatim densos in cellulis corticalibus terminalibus vel subterminalibus formantia. Fila carpogonialia et fila cellulae auxiliaris tunica mucilaginosa crassa carentia. Cellula auxiliaris generativa distinguibilis ante conjugationem cum filo conjunctivo. Cystocarpia subsphericae, laxae constructae, usque 240 µm diametro, fissura carentia. Carposporangia obovoidea, 14-25 µm diametro. Tetrasporophyta ignota.

Plants saxicolous, erect, to 13 cm in height, axes gelatinous, terete, to 5 mm in diameter, irregularly radially branched to five orders, non annulate. Axial cells without crystals. Rhizoidal filaments to 20 µm in diameter, producing terminal adventitious cortical fascicles. Cortical fascicles flexuous, subalternately and dichotomously branched; outer cortical cells cylindrical. Gametophytes dioecious. Spermatangia forming dense paniculate clusters on terminal or subterminal cortical cells. Carpogonial and auxiliary-cell filaments without a thick mucilage coat. Generative auxiliary cell distinct by shape and size before fusion with connecting filament. Cystocarps subsphaerical, loosely constructed, to 240 µm in diameter, not cleft. Carposporangia obovoid, 14-25 µm in diameter. Tetrasporophytes unknown.

Holotype: TFC Phyc 8836 (Fig. 1). Female gametophyte. 3 m depth, Agua Dulce, Los Abrigos, Tenerife, Canary Islands, 27 May 1994; leg. *J. Afonso-Carrillo, M. Sansón, J. Reyes, N. Tabares & M.J. Martín.*

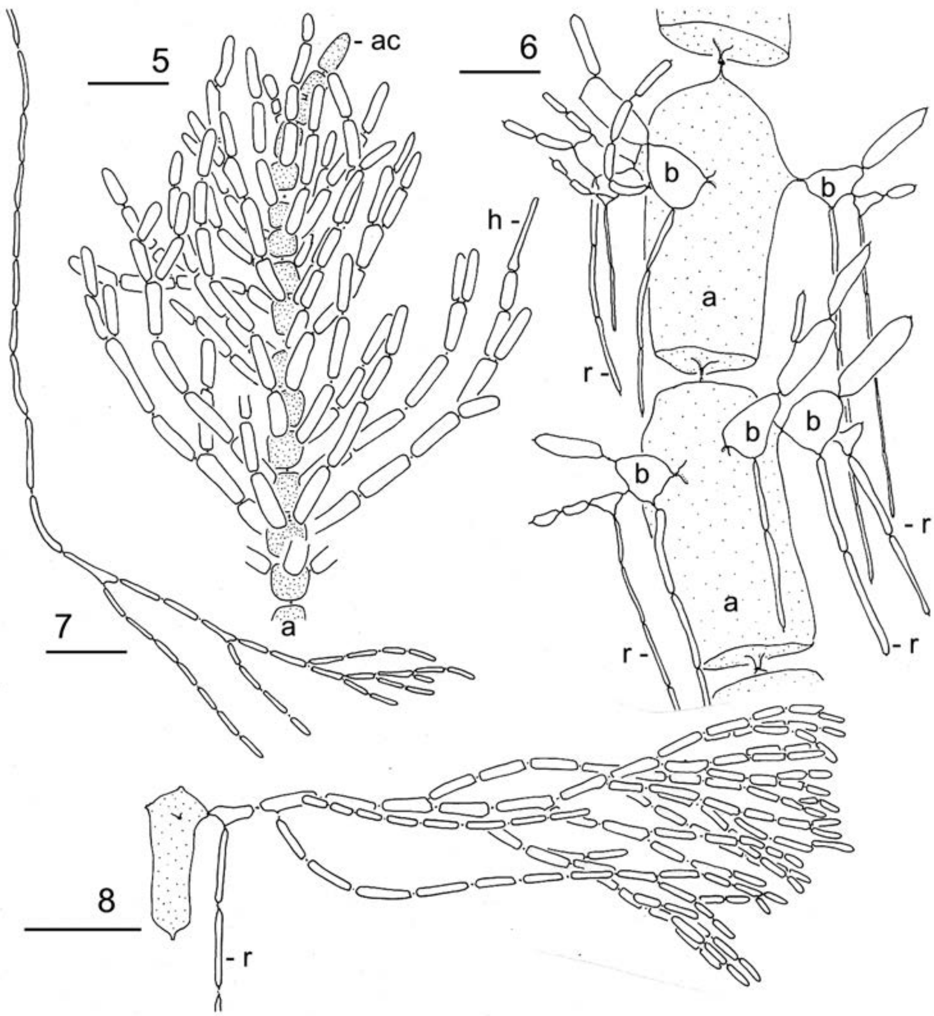
Etymology: The specific epithet honours Isabella A. Abbott, for her extraordinary contribution to phycology, including studies on Hawaiian species of *Dudresnaya* (Abbott, 1996; Abbott & McDermid, 2001).



Figs 1-4. *Dudresnaya abbottiae* Afonso-Carrillo *et* Tabares, sp. nov. (Holotype, TFC Phyc 8836, unless stated). Fig. 1. Holotype specimen. Scale bar = 20 mm. Fig. 2. Branch tip of a mature branch showing numerous cystocarps. Scale bar = 200 µm. Fig. 3. Three successive axial cells (a) bearing cortical fascicles and reproductive filaments scattered throughout the inner cortex: one carpogonial filament (arrowhead) and three auxiliary-cell filaments (arrows). Scale bar = 50 µm. Fig. 4. Cortical filaments bearing terminal spermatangia (TFC Phyc 7423). Scale bar = 50 µm.

Isotype: TFC Phyc 8835. Male gametophyte. 3 m depth, Agua Dulce, Los Abrigos, Tenerife, 27 May 1994; leg. *J. Afonso-Carrillo, M. Sansón, J. Reyes, N. Tabares & M.J. Martín*).

Other specimens examined: TFC Phyc 7423 (male gametophyte; 15 March 1991, El Médano, Tenerife, leg. *J. Reyes*). TFC Phyc 8838 (female gametophyte; 19 May 1994, San Marcos, Icod, Tenerife, leg. *E. Muñoz, J. Reyes &*

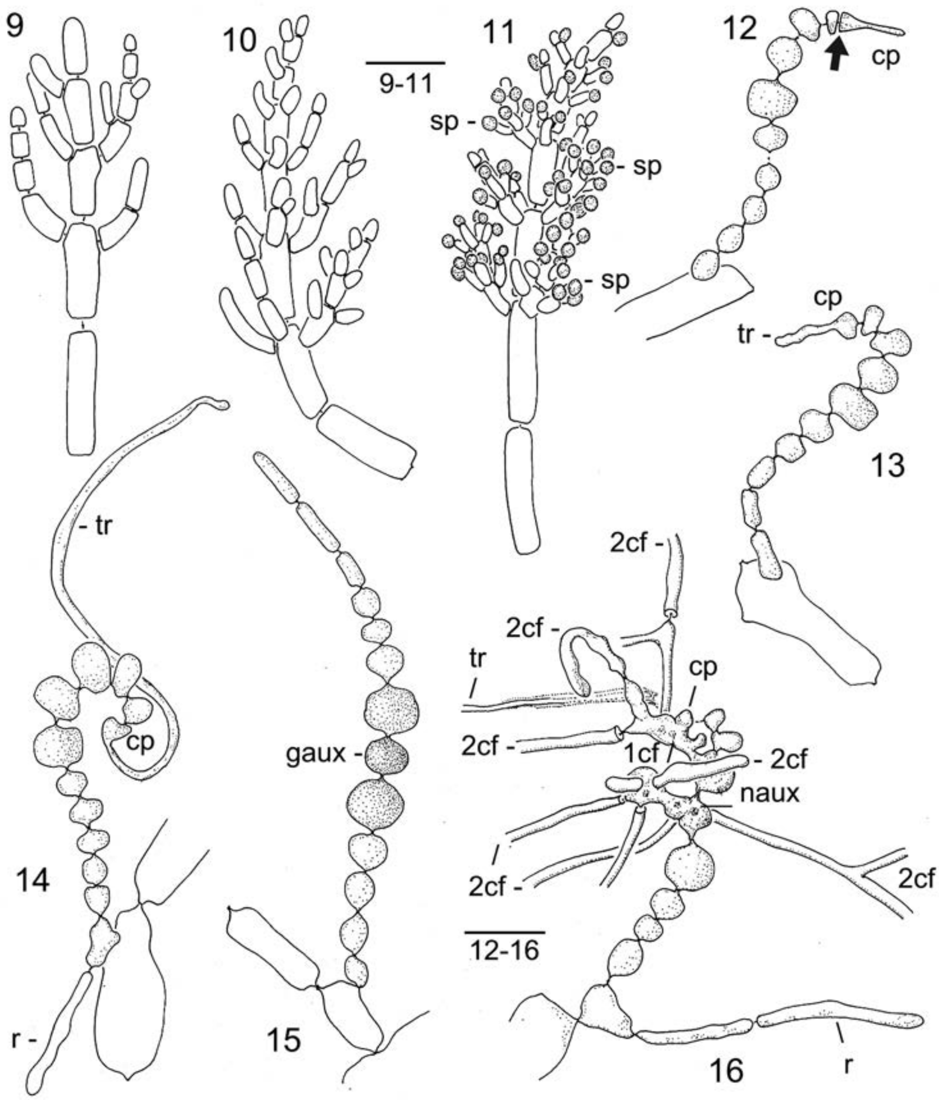


Figs 5-8. *Dudresnaya abbottiae* Afonso-Carrillo *et* Tabares, sp. nov. (Holotype, TFC Phyc 8836). Fig. 5. Percurrent central axis (a) and indeterminate apical cell (ac). Note a floridean hair (h) borne terminally on a cortical filament. Scale bar = 20 µm. Fig. 6. Two successive axial cells (a) each bearing a whorl of cortical fascicles. Note descending rhizoidal filaments (r) arising from basal (b) and proximal cells of fascicles. Scale bar = 50 µm. Fig. 7. Detail of a descending rhizoidal filament that grows towards the outer cortex and ends as a cortical fascicle. Scale bar = 50 µm. Fig. 8. Detail of young fascicle showing cylindrical cortical cells. Scale bar = 50 µm.

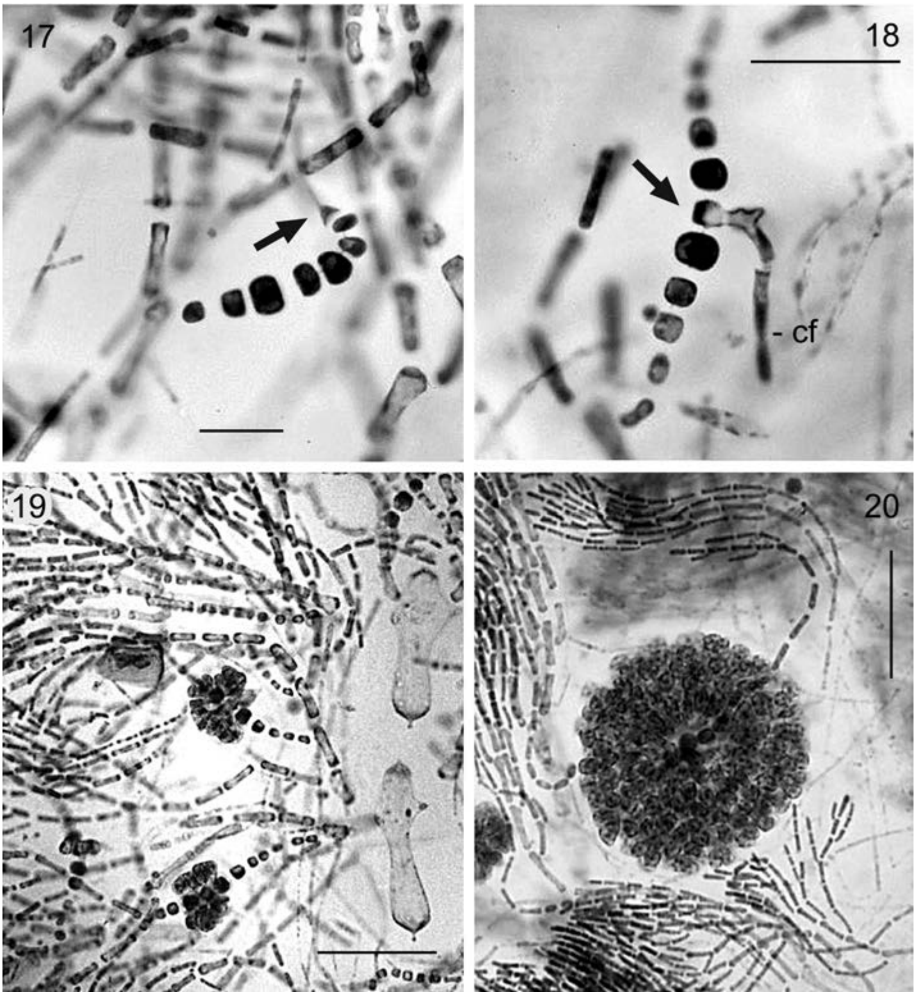
M. Sansón). TFC Phyc 8842 (male gametophyte; 12 June 1994, San Marcos, Icod, Tenerife, leg. *E. Muñoz, J. Reyes & M. Sansón*).

Distribution: Canary Islands: Tenerife.

Habitat: *Dudresnaya abbottiae* grows on cobbles lacking perennial vegetation at depths of 3-7 m. It is a spring annual in areas of moderate water movement and is probably subject to sand abrasion during storm periods.



Figs 9-16. *Dudresnaya abbottiae* Afonso-Carrillo *et* Tabares, sp. nov. (Holotype, TFC Phyc 8836, unless stated). Figs 9, 10. Early developmental stages of spermatangial clusters arising from outermost cortical cells (TFC Phyc 7423). Fig. 11. Mature spermatangial paniculate cluster showing terminal spermatangia (sp) (TFC Phyc 7423). Fig. 12. Carpogonial filament with young carpogonium (cp) after single oblique division (arrow). Fig. 13. Carpogonial filament terminated by an immature carpogonium (cp) with a short trichogyne (tr). Fig. 14. Reflexed carpogonial filament terminated by a mature carpogonium (cp) with rhizoidal filament arising from its proximal cell. Fig. 15. Mature auxiliary-cell filament with generative auxiliary cell (gaux) located between two enlarged cells. Fig. 16. Production of secondary connecting filaments (2cf) from the fusion complex formed by carpogonium (cp), primary connecting filament (1cf) and nutritive auxiliary cells (naux). Scale bar for figures 9-11 = 10 µm, for figures 12-16 = 20 µm.



Figs 17-20. *Dudresnaya abbottiae* Afonso-Carrillo *et* Tabares, sp. nov. (Holotype, TFC Phyc 8836). Fig. 17. Hooked carpogonial filament terminated by mature carpogonium (arrow). Scale bar = 20 µm. Fig. 18. Detail of an auxiliary-cell filament with the generative auxiliary cell (arrow) after its fusion with a connecting filament (cf). Scale bar = 20 µm. Fig. 19. Inner cortex with several auxiliary-cell filaments bearing young gonimoblasts. Scale bar = 100 µm. Fig. 20. A mature cystocarp with carposporangia completely surrounding its auxiliary-cell filament. Scale bar = 100 µm.

Habit: Plants are erect, arising from a single small discoid holdfast, up to 13 cm in height, reddish-brown, gelatinous, smooth and slippery (Fig. 1). One to six main axes, each terete and up to 5 mm diam., arise from the holdfast. Main axes are densely radially branched up to five orders, with laterals forming very acute axils. All laterals are terete and progressively thinner, the highest order near 300 µm diam., nonannulate, and taper gradually to relatively acute apices (Fig. 2).

Vegetative structure: Apical cells of indeterminate axes are subcylindrical, 6-10 µm long and 3-5 µm diam., and cut off subcylindrical axial cells that gradually increase in size up to 400 µm in length and 110 µm in diam. (Fig. 3). Indeterminate axes are clearly percurrent and one or two axial cells behind the apex may remain uncorticated (Fig. 5). Crystalline inclusions are absent. A single whorl of 4-5 cortical fascicles is produced from the distal third of each axial cell (Fig. 6). Cortical fascicles are flexuous, up to twelve times subalternately or dichotomously branched, reaching c. 1000 µm in length. The basal 1-5 cells of cortical fascicles are subcylindrical to obovoid, up to 60 µm in length and 40 µm in diam. (Fig. 6), the remaining outer cortical cells are cylindrical and relatively similar in size. The terminal cells are 7-19 µm long and 3.5-4.5 µm diam. (Fig. 8), and occasionally bear floridean hairs up to 250 µm long (Fig. 5). The successive fascicles are always confluent and all branches lack annulations. An indeterminate axis may occasionally arise from an axial cell in place of a cortical fascicle, repeating the branching pattern of the main axis.

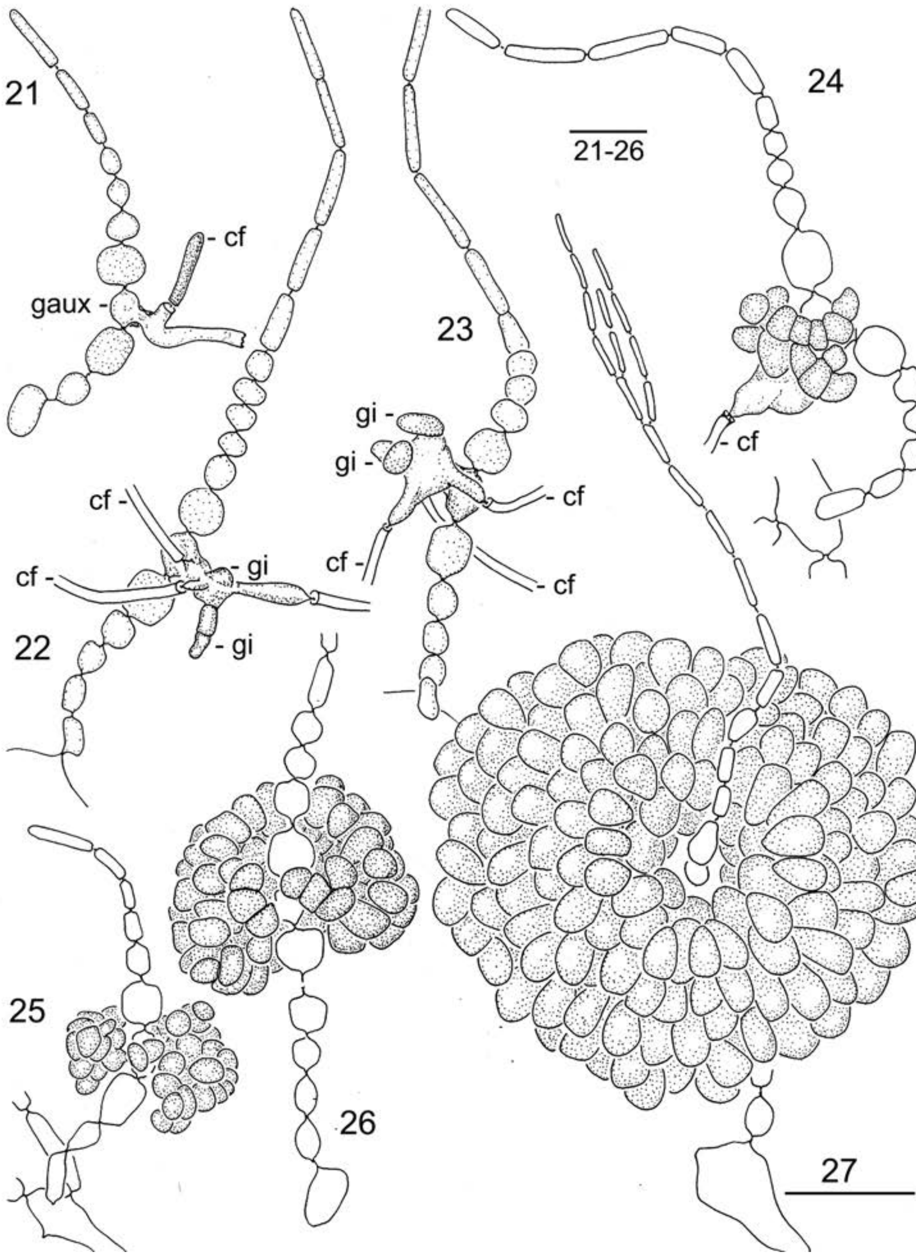
Basal and proximal cells of cortical fascicles produce simple or rarely branched, descending rhizoidal filaments (Figs 6-8) that obscure the indeterminate axes. Rhizoids are very numerous, slender, mostly less than 10 µm diam. (occasionally up to 20 µm diam.), and they do not branch perpendicularly to form secondary cortical filaments. However, descending rhizoids commonly curve outwards, growing into the cortex before branching distally to produce adventitious cortical fascicles (Fig. 7).

Reproduction: Gametophytes are dioecious. Spermatangial clusters are densely paniculate and borne on 2-6 outermost cortical cells (Fig. 4). Spermatangial axes are one to four-celled (Figs 9, 10), bearing a single terminal whorl of three to four spermatangial mother cells, which in turn cut off one to three spherical spermatangia, 2 µm diam. (Fig. 11).

Carpogonial and auxiliary-cell filaments arise in the inner cortex (Fig. 3), in place of vegetative filaments. Carpogonial and auxiliary-cell filaments never produce a thick mucilage coat. The mature carpogonial filament is composed of 6-12 cells, most of them subspherical and darkly staining (Figs 12-14, 17). The third, fourth and fifth cells below the carpogonium are usually larger than the remaining cells of the carpogonial filament. The filament apex becomes hooked as result of unequal elongation of the subterminal cells and an oblique division of the young carpogonium after initiation of the trichogyne (Figs 12-14). A rhizoidal filament arises commonly from the basal cell of carpogonial filaments, but others vegetative laterals were not observed (Fig. 14).

Auxiliary-cell filaments are composed of 8-22 cells, 5-10 of which are rounded and darkly staining (Fig. 15). The generative auxiliary cell is small and lies between two conspicuously inflated cells (Fig. 15), and generally occurs in the central or proximal part of the filament. Unmodified cylindrical cells usually terminate the auxiliary-cell filament, whereas basal cells are always relatively rounded. Auxiliary-cell filaments are simple and never produce sterile laterals or rhizoids on proximal cells.

After fertilization, the base of the trichogyne becomes constricted and the carpogonium produces a primary connecting filament that fuse with either or both cells three and four (nutritive auxiliary cells) below the carpogonium (Fig. 16). Up to ten secondary connecting filaments arise from the resulting fusion (Fig. 16). Secondary connecting filaments fuse laterally with generative auxiliary cells before continuing to effect further diploidizations (Figs 18, 21). The fused portion of connecting filament inflates laterally from the auxiliary cell, and two or three gonimoblast initials and additional connecting filaments are formed



Figs 21-27. *Dudresnaya abbottiae* Afonso-Carrillo *et* Tabares, sp. nov. (Holotype, TFC Phyc 8836). Fig. 21. Generative auxiliary cell (gaux) after fusion with a connecting filament (cf). Figs 22, 23. Early developmental stages of gonimoblasts showing gonimoblast initials (gi) arising from the swollen part of connecting filaments (cf) near its points of fusion with generative auxiliary cells. Figs 24-26. Young cystocarps showing how carposporangial mass progressively encircle the auxiliary-cell filament. Scale bar for figures 21-26 = 20 µm. Fig. 27. A mature cystocarp with carposporangia completely surrounding their auxiliary-cell filament. Scale bar = 50 µm.

(Figs 22, 23). Gonimoblast initials produce a loosely constructed cystocarp that usually grows to encircle the auxiliary-cell filament completely (Figs 19, 20, 24-26). Mature cystocarps are subspherical, up to 240 µm diam., and consist of obovoid carposporangia 14-25 µm diam. (Fig. 27). Simultaneously with cystocarp maturation, auxiliary-cell filaments continue growing and usually branch at their distal portions (Fig. 27).

Tetrasporophytes are unknown.

DISCUSSION

Dudresnaya abbottiae has no single unique feature, but differs from the other species of the genus by a distinctive combination of attributes. The other species of *Dudresnaya* reported from the Canary Islands (*D. canariensis*, *D. crassa*, *D. multiramosa*, and *D. verticillata*) are different in several vegetative and reproductive features (Tab. 1). *Dudresnaya abbottiae* and *D. canariensis* show some likeness in external appearance, but the former can be distinguished by its slender young branches ending in acute apices. In addition, the new species can readily be separated vegetatively and reproductively from *D. canariensis*, by its axial cells lacking hexagonal crystalline inclusions, percurrent apex of indeterminate axes, slender rhizoids (< 20 µm *vs* up to 95 µm) that terminally produce adventitious cortical filaments, carpogonial branches that bear rhizoids, cystocarps loosely constructed that completely encircle the auxiliary-cell filaments, and paniculate clusters rather than corymbose spermatangial mother cells (Tabares *et al.*, 1997).

Dudresnaya crassa, *D. multiramosa* and *D. verticillata* have annulations in the younger branches and are easily distinguished in external appearance from *D. abbottiae*. In addition, *Dudresnaya crassa* also differs by its obscure apex of indeterminate axes, slender rhizoids (< 7 µm) which do not produce adventitious cortical filaments, thick mucilage coat around reproductive filaments, sterile laterals on lower cells of auxiliary-cell filaments, and spermatangial mother cells arranged in opposite pairs (Taylor, 1950; Robins & Kraft, 1985; Schneider & Searles, 1991). The recently described *Dudresnaya multiramosa* has ellipsoid rather than cylindrical outer cortical cells, trichotomously to pentachotomously branched cortical fascicles, multilobed cystocarps, and spermatangial mother cells borne singly or in pairs on terminal and penultimate cortical cells (Afonso-Carrillo *et al.*, 2002). *Dudresnaya verticillata* also differs in possessing hexagonal crystals in the axial cells, thicker rhizoids (up to 40 µm) that produce laterally and perpendicularly rather than terminally adventitious cortical filaments, carpogonial and auxiliary-cell filaments that bear vegetative cortical laterals but do not produce rhizoids, the consistent double oblique carpogonial division, and compactly constructed cystocarps (Bornet & Thuret, 1876; Robins & Kraft, 1985).

Dudresnaya abbottiae also differs from the remaining Atlantic species, which have been reported only from western Atlantic coasts. From *Dudresnaya bermudensis*, *D. georgiana* and *D. puertoricensis* it differs mainly in having cylindrical rather than subspherical outer cortical cells [for additional features see table of characteristics in Afonso-Carrillo *et al.* (2002)]. *Dudresnaya patula* has compressed axes, rhizoids that do not produce adventitious cortical filaments, and cystocarps that incompletely surround the auxiliary-cell filament leaving a narrow cleft (Eiseman & Norris, 1981).

Table 1. Comparison of *Dudresnaya abbottiae* Afonso-Carrillo *et* Tabares sp. nov. and eastern Atlantic and related species.

Character	*D. abbottiae*	*D. babbittiana*[1]	*D. canariensis*[2]	*D. capricornica*[3]	*D. crassa*[4]	*D. kuroshioensis*[5]	*D. multiramosa*[6]	*D. verticillata*[7]
Distribution	Canary Islands	Midway Atoll	Canary Islands	Australia, Arabian Sea	Western Atlantic, Azores, Canary Islands	Japan	Canary Islands Mediterranean,	NE Atlantic, Canary Islands
Max. height of habit (cm)	13	10-18	8.5	11	25	20	12	26
Major branches	terete	terete	terete	terete	terete	terete	terete	terete
Max. diameter of branches (mm)	5	5	7	10	10	10	3	2
Annulations	absent	absent	absent	absent	present	absent	present	present
Hexagonal crystals	absent	present	present	present	no data	present	absent	present
Apex of indeterminate axes	protuberant	no data	obscure	protuberant or obscure	obscure	protuberant	protuberant	protuberant
Shape of outer cortical cells	cylindrical	cylindrical	cylindrical	cylindrical	cylindrical	cylindrical	ellipsoid	cylindrical
Branching of cortical fascicles	subalternate and trichotomous	dichotomous and trichotomous	dichotomous and trichotomous	secund and in all directions	dichotomous to alternate	dichotomous (rarely trichotomous)	trichotomous to pentachotomous	dichotomous and trichotomous
Adventitious cortical filaments arising from rhizoids	as terminal fascicles	absent	absent	absent	absent	absent	absent	as perpendicular laterals
Max. diameter of rhizoids (µm)	20	2	95	85	7	21	60	40
Arrangement of spermatangial mother cells	paniculate clusters	unknown	corymbose fascicles	lateral whorls	opposite pairs	unknown	singly or in pairs	terminal clusters
Site of reproductive filaments	inner cortex	inner and middle cortex	middle cortex	inner cortex	inner cortex	inner cortex	inner cortex	inner cortex
Mucilage coat	absent	absent	absent	absent	present	absent	absent	absent

Character	*D. abbottiae*	*D. babbittiana*[1]	*D. canariensis*[2]	*D. capricornica*[3]	*D. crassa*[4]	*D. kuroshioensis*[5]	*D. multiramosa*[6]	*D. verticillata*[7]
Carpogonial filaments bearing sterile laterals	absent	absent	absent	absent	present	present	absent	present
Carpogonial filaments bearing rhizoids	present	absent	absent	present	absent	absent	absent	absent
Oblique divisions of carpogonium	1	no data	1	0-1	no data	0-1	1	2
Auxiliary-cell filaments bearing sterile laterals	absent	absent	absent	present	present	present	absent	present
Auxiliary cell distinctly smaller than adjacent cells	present	absent	present	absent	present	absent	present	present
Shape of cystocarp	subspherical	subspherical	subspherical	subspherical	subspherical	spherical	multilobed	subspherical
Max. diameter of cystocarps (μm)	240	150	245	250	320	210	200	170
Cystocarp cleft	absent	absent	present	absent	no data	present	present	absent
Carposporangia arrangement	loose	no data	compact	loose	no data	loose	compact	compact
Size of carposporangia (μm)	14-25	14	15-25 × 8-10	25	7.5-15	10-26 × 7-13	10-15	20
Tetrasporophyte	unknown	isomorphic	unknown	isomorphic	isomorphic	isomorphic	unknown	isomorphic
Gametophyte	dioecious	dioecious	dioecious	monoecious	dioecious	dioecious	monoecious	monoecious

1. Data from Abbott & McDermid (2001).
2. Data from Tabares *et al.* (1997).
3. Data from Robins & Kraft (1985).
4. Data from Taylor (1950) and Schneider & Searles (1991).
5. Data from Kajimura (1994).
6. Data from Afonso-Carrillo *et al.* (2002).
7. Data from Bornet & Thuret (1876, as *Dudresnaya coccinea* Crouan) and Robins & Kraft (1985)

Among the non-Atlantic species, *Dudresnaya abbottiae* seems most closely related to *D. babbittiana* Abbott *et* McDermid from Midway Atoll, North Central Pacific (Abbott & McDermid, 2001), *D. capricornica* Robins *et* Kraft from Australia and Arabian Sea (Robins & Kraft, 1985; Schils & Coppejans, 2002), and *D. kuroshioensis* Kajimura from Japan (Kajimura, 1994). These species show some similarities in overall habit and shape of outer cortical cells, and they are also compared in Table 1. Of these, *Dudresnaya babbittiana* differs by possessing hexagonal crystals in the axial cells, slender rhizoids (< 2 µm) that do not produce adventitious cortical filaments, carpogonial filaments that do not bear rhizoids, auxiliary cells that are indistinguishable from adjacent cells prior to diploidization, and smaller cystocarps and carposporangia (Abbott & McDermid, 2001). *Dudresnaya capricornica* has hexagonal crystalline inclusions in the axial cells, thicker rhizoids (< 85 µm) that do not produce adventitious cortical filaments, auxiliary-cell filaments that bear vegetative laterals, auxiliary cells that are indistinguishable before contact with a connecting filament, and double-whorled lateral spermatangial mother cells (Robins & Kraft, 1985). *Dudresnaya kuroshioensis* differs by possessing hexagonal crystals in axial cells, rhizoids that do not produce adventitious cortical filaments, carpogonial and auxiliary-cell filaments that bear cortical laterals but do not produce rhizoids, auxiliary cells that are indistinguishable before contact with a connecting filament, and cystocarps that incompletely surround the auxiliary-cell filament (Kajimura, 1994).

In conclusion, *Dudresnaya abbottiae* seems closely related to the Canarian *D. canariensis* and the Indo-Pacific *D. babbittiana*, *D. capricornica* and *D. kuroshioensis*, all of them without autapomorphic characters, but differing by their unique combinations of significant attributes. Among the characters used in species delineation, the arrangement of spermatangia seems to have a high diagnostic value. Although in *Dudresnaya babbittiana* and *D. kuroshioensis* male gametophytes remain unknown, in *D. canariensis* spermatangia are formed in corymbose terminal fascicles (Tabares *et al.,* 1997), in *D. capricornica* they are arranged in lateral whorls (Robins & Kraft, 1985), whereas in *D. abbottiae* they occur in terminal paniculate clusters. These noticeable differences in arrangement of spermatangial mother cells support the retention of these species as closely related but distinct.

With the addition of *Dudresnaya abbottiae*, nineteen species are currently included in the genus. These are separated by the following key, which is based on keys presented by Robin & Kraft (1985) and Kajimura (1993, 1994) and are herein modified to accommodate all presently accepted *Dudresnaya* species.

Key to species of the genus *Dudresnaya* P.L. *et* H.M. Crouan

1a. Distal cells of cortical fascicles subspherical to ellipsoid 2
1b. Distal cells of cortical fascicles cylindrical 7
 2a. Annulations present in young branches 3
 2b. Annulations absent in young branches 5
3a. Generative auxiliary cell similar in diameter to adjacent cells; sterile laterals present on proximal cells of carpogonial and auxiliary-cell filaments; cortical fascicles dichotomously branched 4
3b. Generative auxiliary cell distinctly smaller than adjacent cells; sterile laterals absent on proximal cells of carpogonial and the auxiliary-cell filaments; cortical fascicles trichotomously to pentachotomously branched . . . . *D. multiramosa* Afonso-Carrillo, Sansón *et* Reyes

4a. Axial cells with rectangular crystalline inclusions; rhizoids almost never producing adventitious cortical laterals; mature cystocarp up to 140 μm diam. . . . . *D. puertoricensis* Searles *et* Ballantine
4b. Axial cells without hexagonal crystals; rhizoids regularly producing perpendicular laterals that become adventitious cortical fascicles; mature cystocarp up to 430 mm diam.. . . . . *D. littleri* Abbott
5a. Generative auxiliary cell distinctly smaller than adjacent cells; distal cells of cortical fascicles moniliform . . . . *D. bermudensis* Setchell
5b. Generative auxiliary cell similar in diameter to adjacent cells; distal cells of cortical fascicles ellipsoid or cylindrical to ellipsoid 6
6a. Major branches terete or compressed; distal cells of cortical fascicles ellipsoid; gonimoblast initials arising from the auxiliary cell; plants dioecious . . . . *D. colombiana* Taylor
6b. Major branches terete and villose; distal cells of cortical fascicles cylindrical to ellipsoid; gonimoblast initials arising from the connecting filament near the junction with auxiliary cell; plants monoecious . . . . *D. georgiana* Searles
7a. Main axes of plants broadly flattened (to 3 mm thick by 20 mm wide). . . . . *D. patula* Eiseman *et* Norris
7b. Main axes of plants not broadly flattened 8
8a. Annulations present in young branches. 9
8b. Annulations absent in young branches 13
9a. Rhizoids regularly producing perpendicular laterals that become adventitious cortical fascicles 10
9b. Rhizoids simple or laxly pseudodichotomous, almost never producing adventitious cortical fascicles 12
10a. Indeterminate axes arising in inner cortex as unbranched primordia of up to 40 discoid cells; young carpogonium undergoes a single oblique division . . . . *D. australis* J. Agardh *ex* Setchell
10b. Indeterminate axes arising by modification of normal cortical fascicles, distinct primordia absent; young carpogonium generally undergoes two oblique divisions 11
11a. Plants up to 26 cm in length; axial cells with hexagonal crystals; carposporangia completely encircling auxiliary-cell filament; tetrasporophyte isomorphic . . . . *D. verticillata* (Withering) Le Jolis
11b. Plants up to 4 cm in length; axial cells without hexagonal crystals; carposporangia not completely encircling auxiliary-cell filament; tetrasporophyte heteromorphic (a polystromatic crust) . . . . *D. minima* Okamura
12a. Mucilage coat present around carpogonial and auxiliary-cell filaments; rhizoids up to 7 mm diam. *D. crassa* Howe
12b. Mucilage coat absent around carpogonial and auxiliary-cell filaments; rhizoids up to 36 mm diam. . . . . *D. okiensis* Kajimura
13a. Plants small, up to 4 cm in length; distal cells of cortical fascicles ranging from cylindrical to ellipsoid . . . . *D. georgiana* Searles
13b. Plants generally larger, up to 20 cm in length; distal cells of cortical fascicles exclusively cylindrical 14
14a. Mucilage coat present around carpogonial and auxiliary-cell filaments 15
14b. Mucilage coat absent around carpogonial and auxiliary-cell filaments 16
15a. Branches and main axes generally somewhat compressed; branching irregular and radial; plants monoecious . . . . *D. hawaiiensis* R.K.S. Lee
15b. Branches and main axes generally terete; branching irregularly di-/trichotomous; plants dioecious . . . . *D. japonica* Okamura

16a. Rhizoids up to 2 µm diam.; mature cystocarps less than 150 µm diam. composed by carposporangia 14 µm diam. . . . . *D. babbittiana* Abbott *et* McDermid
16b. Rhizoids up to 21-91 µm diam.; mature cystocarps more than 200 µm diam. formed by carposporangia up to 25 µm diam. 17
17a. Carposporangia completely encircling auxiliary-cell filament 18
17b. Carposporangia not completely encircling auxiliary-cell filament 19
18a. Axial cells with hexagonal crystals; rhizoids almost never producing adventitious cortical fascicles; spermatangia produced on lateral whorls; plants monoecious . . . . *D. capricornica* Robins *et* Kraft
18b. Axial cells without hexagonal crystals; rhizoids regularly producing terminal adventitious cortical fascicles; spermatangia produced on terminal paniculate clusters; plants dioecious . . . . *D. abbottiae* Afonso-Carrillo *et* Tabares
19a. Plants up to 8.5 cm in length; maximum diameter of rhizoids 95 µm; carpogonial and auxiliary-cell filaments arise in the middle cortex; spermatangia produced in corymbose fascicles . . . . *D. canariensis* Tabares, Afonso-Carrillo, Sansón *et* Reyes
19b. Plants up to 20 cm in length; maximum diameter of rhizoids 21 µm; carpogonial and auxiliary-cell filaments arise in the inner cortex; spermatangia unknown. . . . . *D. kuroshioensis* Kajimura

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