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Vegetative and reproductive morphology of *Dudresnaya canariensis* sp. nov. (Dumontiaceae, Rhodophyta)

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The marine red alga *Dudresnaya canariensis* sp. nov. (Dumontiaceae, Gigartinales) from the Canary Islands is described. Gametophytes are terete and radially branched, young branches are nonannulate, outer cortical cells are cylindrical, axial cells contain hexagonal crystals, cells of primary axes are conspicuous, and rhizoids reach 95 μm in diameter. Spermatangial mother cells occur in corymbose clusters on the outer cortex, and carpogonial and auxiliary-cell filaments, both of which lack a thick mucilage coat, arise in the mid-cortex. Carpogonial filaments are reflexed, the carpogonium and trichogyne differentiating after final oblique division. The gonimoblast initials do not recurve around the auxiliary-cell filament, and the cystocarps are distinctly cleft. Tetrasporophytes are unknown. The only unique feature of *D. canariensis* is the arrangement of its spermatangia in corymbose terminal and subterminal fascicles, a feature unreported in the few species of *Dudresnaya* where male gametophytes are known. However, *D. canariensis* differs from the other *Dudresnaya* species by a unique combination of significant attributes. It is postulated that the Australian *D. capricornica* and the Japanese *D. kuroshioensis* are the closest relatives of the new species.

INTRODUCTION

The genus *Dudresnaya* was established by P.L. & H.M. Crouan (1835) and includes uniaxial, soft, gelatinous, irregularly branched algae with simple carpogonial and auxiliary-cell filaments that are morphologically distinct and spatially separated (Kylin 1928). In the past, species of *Dudresnaya* were mostly characterized by external morphology. However, Robins & Kraft (1985) proposed that species could best be defined by a combination of features: (1) external ones such as habit, branching pattern, and presence or absence of annulations in young branches; (2) internal vegetative features such as the shape of outer cortical cells, the presence or absence of hexagonal crystals in axial cells, the prominence of central-axial cells, the diameters of rhizoids, the presence or absence of adventitious cortical laterals on rhizoidal filaments, the prominence of indeterminate-axis primordia, and floridean hairs; and (3) reproductive characters such as the presence or absence of a discernible mucilage coat around carpogonial and auxiliary-cell filaments, the anatomy of spermatangial axes, the number of oblique divisions preceding formation of the carpogonium, the initial direction and orientation of gonimoblast initials, the prominence of longitudinal clefts in the cystocarps, and the type of life history. Searles & Ballantine (1986) and Kajimura (1993, 1994) have followed these criteria in describing new species.

Fifteen species of *Dudresnaya* are currently recognized (Robins & Kraft 1985; Kajimura 1994), most of them from warm seas where they are generally sublittoral and ephemeral spring–summer annuals. *Dudresnaya verticillata* (Withering) Le Jolis has been widely reported from the eastern Atlantic and the Mediterranean (Irvine 1983; South & Tittley 1986), *D. crassa* Howe is known from both the eastern and western Atlantic (Howe 1905; Taylor 1950; Searles 1983; Afonso-Carrillo & Sansón 1989), and *D. hawaiiensis* R.K.S. Lee is recorded from Hawaii and the southwest Pacific (Lee 1963; Robins & Kraft 1985). The remaining species have been infrequently reported and appear to have very restricted distributions: *D. japonica* Okamura (1908), *D. minima* Okamura (1932), *D. okiensis* Kajimura (1993) and *D. kuroshioensis* Kajimura (1994) from Japan; *D. australis* J. Agardh *ex* Setchell (1912) and *D. capricornica* Robins et Kraft (1985) from Australia; *D. lubrica* Littler (1974) from Hawaii; *D. colombiana* Taylor (1945) from Colombia and California; *D. bermudensis* Setchell (1912) from Bermuda and the Bahama Islands; *D. patula* Eiseman et J. Norris (1981) from Florida (USA); *D. georgiana* Searles (1983) from Georgia (USA); and *D. puertoricensis* Searles et Ballantine (1986) from Puerto Rico and Georgia. Specimens recently collected from the Canary Islands differ from all previously described species in their unique combination of morphological and anatomical attributes and are thus recognized as the new species described in this paper. It is the third *Dudresnaya* to be reported from the Canary Islands, together with *D. verticillata* and *D. crassa* (Afonso-Carrillo & Sansón 1989), two species rarely collected as seasonal ephemerals on sublittoral cobbles or small boulders, although recent collections suggest that more species may be present.

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 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 AND DISCUSSION

Dudresnaya canariensis Tabares, Afonso-Carrillo, Sansón et Reyes, sp. nov.

Figs 1–25

DIAGNOSIS: Thallus saxicola, erectus usque ad 8.5 cm altus, lubricus, cylindricus usque ad 7 mm diametro, radiatim ramificatus, ramis iuvenibus sine annulis. Apices axibus indeterminatis occulti ob filamenta corticalia ambientia. Cellulae axiales sat evolutae crystalla hexagona continentes. Fasciculi corticales ramificati pseudotrichotome in partibus internis, ramificatione exoriente pseudodichotoma; cellulis corticalibus externis cylindris. Fila rhizoidealia usque 95 μm diametro. Gametophyta dioica. Spermatangia corymbose fasciculata super cellulas corticales extimas. Fila carpogonialia et fila cellulae auxiliaris tunica mucilagina crassa carentia. Carpogonium iuvene unicam divisionem obliquam subiens, ut apex filo carpogoniali maturo valde reflexus est. Primordia gonimoblastorum circum filamentum cellulae auxiliaris non recurvata. Cystocarpia confertim extructa manifestam fissuram continentia. Tetrasporophyta ignota.

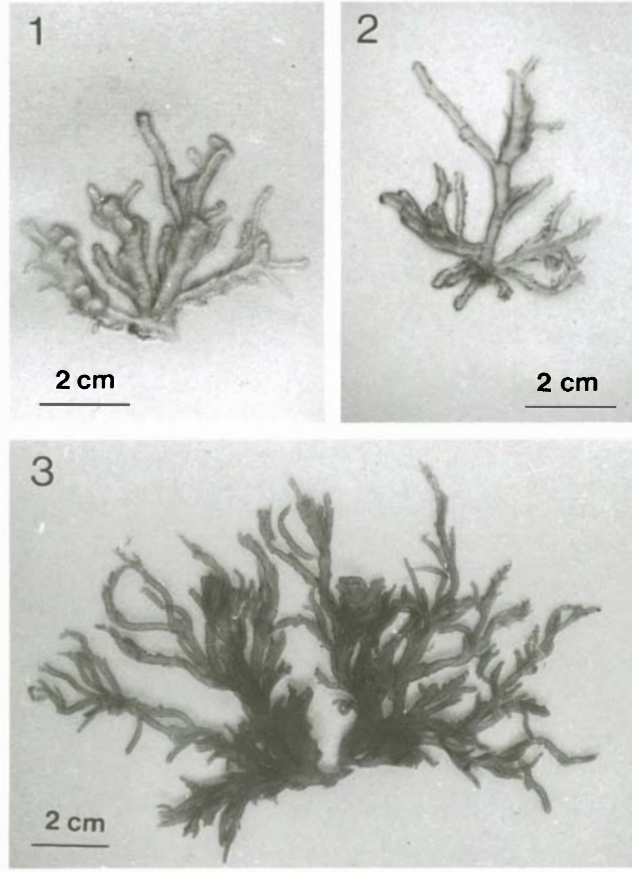
Thalli saxicolous, erect, to 8.5 cm in height, the axes lubricous, terete, to 7 mm in diameter, radially branched, without annulations in young branches. Apices of indeterminate axes obscured by surrounding cortical filaments. Hexagonal crystals present in mature axial cells. Cortical fascicles branched pseudotrichotomously in their proximal portions, pseudodichotomously distally; outer cortical cells cylindrical. Rhizoidal filaments to 95 μm in diameter. Gametophytes dioecious. Spermatangia in corymbose fascicles on the outermost cortical cells. Carpogonial and auxiliary-cell filaments without a thick mucilage coat. Young carpogonia undergoing a single oblique division, causing the apex of the mature carpogonial filament to be strongly reflexed. Gonimoblast initials not recurving around the auxiliary-cell filament. Cystocarps compactly constructed, distinctly cleft. Tetrasporophytes unknown.

HOLOTYPE: TFC Phyc 8837 (Fig. 1). Female gametophyte; 10 m depth, Playa de San Marcos, Icod, Tenerife, Canary Islands, 13.vi.1994; leg. *J. Reyes, M. Sansón & E. Muñoz.*

ETYMOLOGY: The specific epithet refers to the Canary Islands, which is the type locality.

ISOTYPE: TFC Phyc 8845, male, 10 m depth, Playa de San Marcos, Icod, Tenerife, Canary Islands, (13.vi.1994; leg. *J. Reyes, M. Sansón & E. Muñoz*).

REPRESENTATIVE SPECIMENS EXAMINED: Female, 9–10 m depth (*J. Reyes, M. Sansón & E. Muñoz,* 14.vi.1994, TFC Phyc 8844, 8847, 8922); female, 12 m depth (*J. Reyes & N. Tabares,* 16.vi.1995, TFC Phyc 9623).



Figs 1–3. *Dudresnaya canariensis* sp. nov.
Fig. 1. Holotype (TFC Phyc. 8837).
Fig. 2. Male gametophyte (Isotype, TFC Phyc. 8845).
Fig. 3. Liquid-preserved female gametophyte (TFC Phyc. 8922).

DISTRIBUTION: Known only from the type locality.

HABITAT: The species grows at 9–12 m depths on the border of rocky bottoms colonized by a perennial vegetation, mainly of the brown alga *Zonaria tournefortii* (Lamouroux) Montagne, just above sand flats. The rocks inhabited by *Dudresnaya canariensis* are in areas of relatively high water movement and are probably subject to sand abrasion during storm periods, particularly during the autumn and winter. Other ephemeral red algae occurring in this habitat include: *Acrosymphyton purpuriferum* (J. Agardh) Sjöstedt, *Helminthocladia calvadosii* (Lamouroux *ex* Duby) Setchell, *Naccaria wiggii* (Turner) Endlicher, *Scinaia complanata* (Collins) Cotton, and *Thuretella schousboei* (Thuret) Schmitz.

HABIT: Plants are erect from a single discoid holdfast, 8.5 cm in height, gelatinous, lubricous, and irregularly radially

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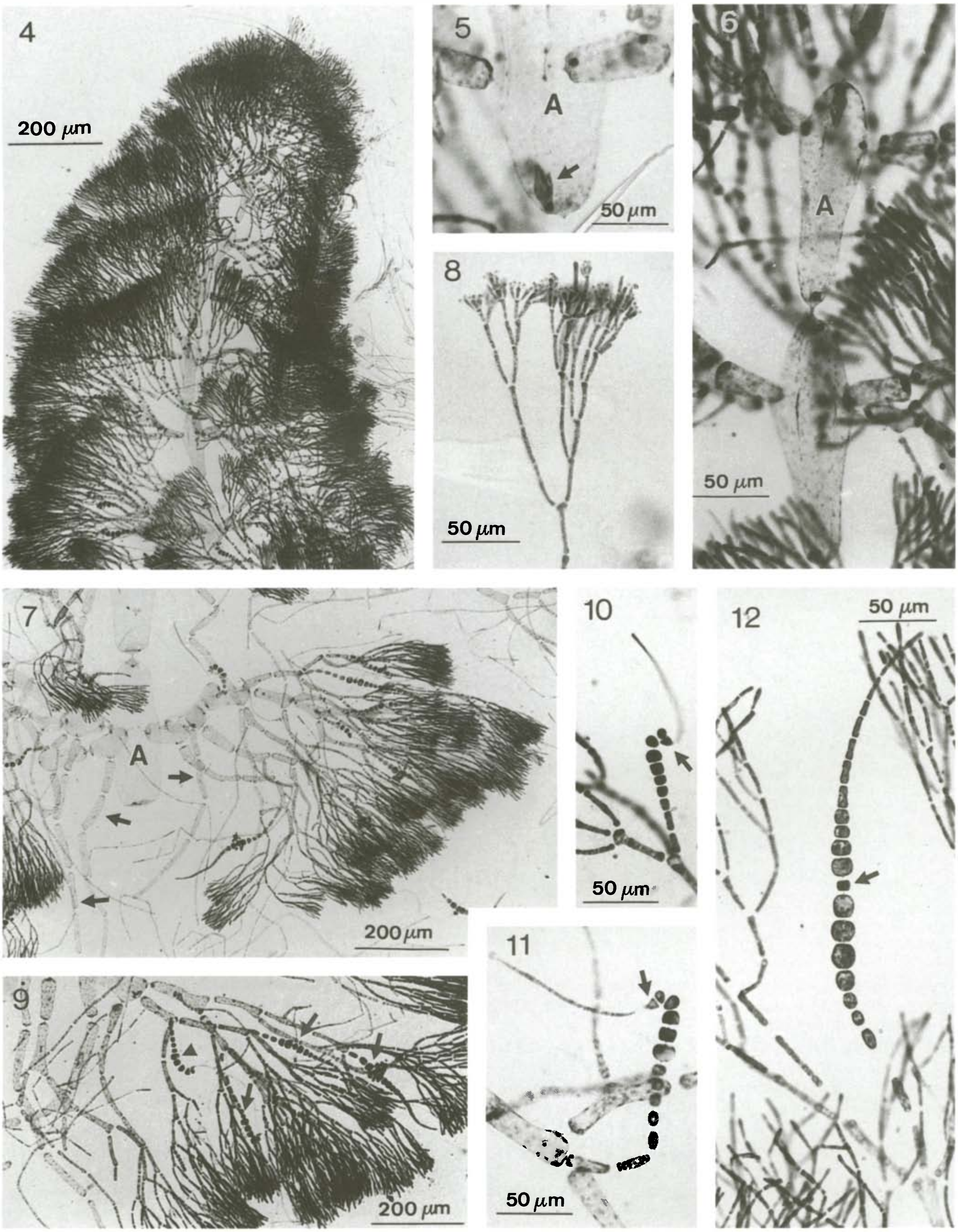
Figs 4–12. *Dudresnaya canariensis* sp. nov. (Holotype, TFC Phyc. 8837, unless stated).
Fig. 4. Young branch showing axial cells and cortical fascicles.
Fig. 5. Axial cell (A) with a single hexagonal crystal (arrow).
Fig. 6. Two successive axial cells (A) each bearing a whorl of cortical fascicles.
Fig. 7. Axial cell (A) bears two cortical fascicles, rhizoidal filaments (arrows) arising from proximal cells of fascicles.
Fig. 8. Cortical filaments bearing terminal spermatangia (Isotype, TFC Phyc. 8845).
Fig. 9. Cortical fascicle showing a carpogonial filament (arrowhead) and auxiliary-cell filaments (arrows) developing in the middle cortex.
Figs 10, 11. Reflexed carpogonial filaments terminated by mature carpogonia (arrows).
Fig. 12. Mature auxiliary-cell filament with an intercalary generative auxiliary cell (arrow).


4
200 μm
5
A
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11
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9
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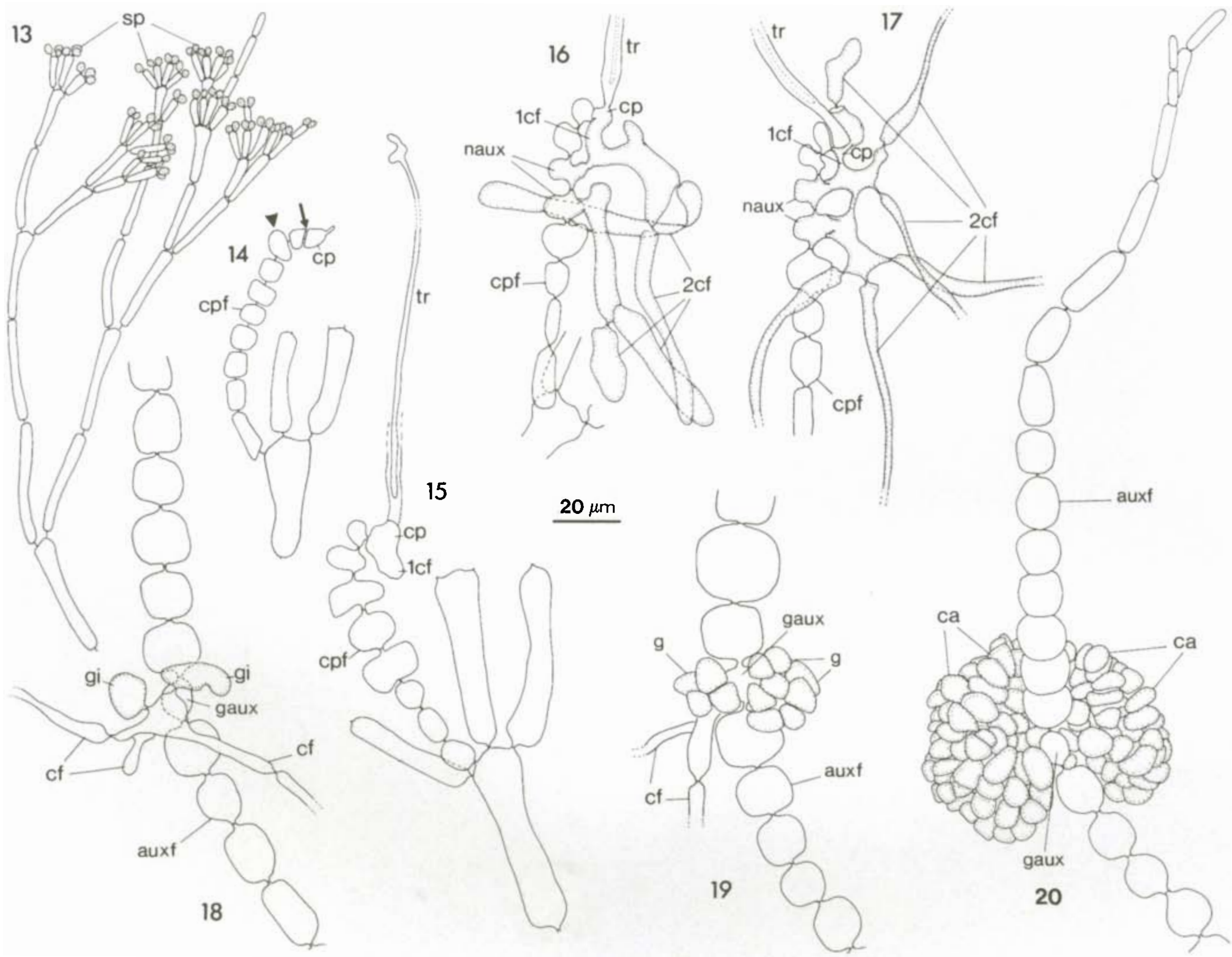
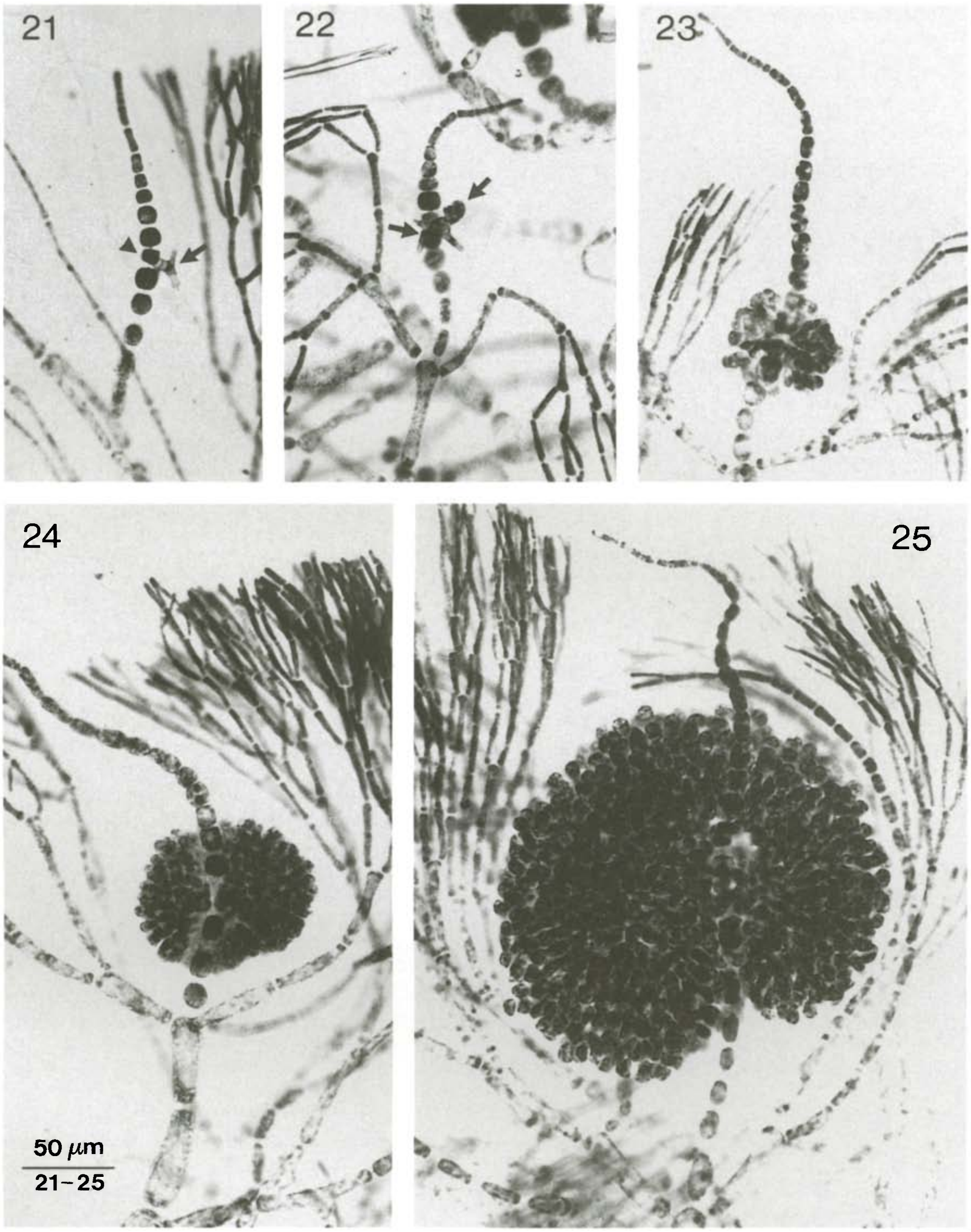


Figs 13–20. *Dudresnaya canariensis* sp. nov. (Holotype, TFC Phyc. 8837, unless stated).
Fig. 13. Cortical filaments bearing spermatangia (sp). (Isotype, TFC Phyc. 8845).
Fig. 14. Carpogonial filament (cpf) with young carpogonium (cp) after single oblique division (arrow). Note unequal elongation of the second cell (arrowhead) below the carpogonium.
Fig. 15. Carpogonial filament (cpf) showing early postfertilization development of the carpogonium (cp), which is initiating a primary connecting filament (1cf).
Figs 16, 17. Production of secondary connecting filaments (2cf) from the fusion complex formed by carpogonium (cp), primary connecting filament (1cf), and nutritive auxiliary cells (naux).
Fig. 18. Detail of an auxiliary-cell filament (auxf) with the generative auxiliary cell (gaux) after its fusion with a connecting filament (cf), from part of which two gonimoblast initials (gi) have arisen.
Fig. 19. Early development of gonimoblasts (g).
Fig. 20. Young cystocarp with carposporangia (ca), the carposporangial mass not completely encircling the auxiliary-cell filament (auxf).

branched. Branching is up to four orders, the laterals occasionally slightly constricted at their bases and forming acute axils. Main axes terete, to 7 mm in diameter; the highest order branches 1–3 mm in diameter, nonannulate, tapering gradually to relatively obtuse apices (Figs 1–3). Plants are light pink in color.

VEGETATIVE STRUCTURE: Apical cells of indeterminate axes are 8–11 μm in length, 3–4 μm in diameter, and are obscured by surrounding and overtopping cortical filaments (Fig. 4). Axial cells gradually increase in size, ultimately reaching 700 μm in length and 120 μm in diameter. One or more hexagonal crystals often occur in well-developed axial cells (Fig. 5). Each axial cell produces a single whorl of 4–5 cortical fascicles (Fig. 6). The successive fascicles are confluent, reach at least c. 1000 μm in length and bi-/trifurcate to 12 times. Inner portions in mature fascicles are relatively consistently pseudotrichotomous (rarely pseudotetrachotomous) and with wide branching angles (> 60°) and subcylindrical cells (to 225 μm long and 125 μm in diameter) that become progressively smaller distally (Figs 7, 9). In outer portions of fascicles the filaments are lax and pseudodichotomously branched at more acute angles (< 45°); outer cortical cells are cylindrical, the terminal cells 5–20 μm long and 2.4–3.5 μm in diameter, commonly bearing floridean hairs up to 175 μm long. Indeterminate branches occasionally arise from axial cells in place of a cortical filament, repeating the branching pattern of the main axes.



Figs 21–25. *Dudresnaya canariensis* sp. nov. (Holotype, TFC Phyc. 8837).
Fig. 21. Generative auxiliary cell (arrowhead) after fusion with a connecting filament (arrow).
Fig. 22. Two gonimoblast initials (arrows) arising from the swollen part of a connecting filament near its point of fusion with a generative auxiliary cell.
Fig. 23. The mostly unilateral development of a young carposporophyte.
Figs 24, 25. A mature cystocarp incompletely surrounding the auxiliary-cell filament to which it is anchored.

Basal and proximal cells of cortical fascicles produce descending rhizoidal filaments that obscure the central axis (Fig. 7). Rhizoids are up to 95 μm in diameter, rarely pseudodichotomously branched, and never giving rise to secondary cortical laterals.

REPRODUCTION: Gametophytes are dioecious. One to three subspherical spermatangia, 2–3 μm in diameter, occur on elongate spermatangial mother cells arranged in corymbose fascicles on the outermost one or two cortical cells (Figs 8, 13).

Table 1. Comparison of *Dudresnaya canariensis* sp. nov. and related species.

Features	*D. canariensis*	*D. capricornica*[1]	*D. kuroshioensis*[2]
Distribution	Canary Islands	Australia	Japan
Habitat	epilithic	epilithic	epilithic
Major branches	terete	terete	terete
Branching	radial	radial	radial
Annulations	absent	absent	absent
Hexagonal crystals	present	present	present
Hairs	present	present	present
Distinct primary axes	present	present	present
Shape of outer cortical cells	cylindrical	cylindrical	cylindrical
Rhizoids bearing cortical laterals	absent	absent	absent
Maximum diameter of rhizoids (μm)	95	85	21
Oblique divisions of carpogonium	1	0–1	0–1
Mucilage coat	absent	absent	absent
Double whorled spermatangial filaments	absent	present	?
Recurved gonimoblast initials	absent	present	present or absent
Cystocarp distinctly cleft	present	absent	present
Alternation of generations	?	isomorphic	isomorphic
Maximum diameter of branches (mm)	7	10	10
Apex of indeterminate axes	obscure	protuberant or obscure	protuberant
Branching of cortical fascicles	pseudotrichotomous and pseudodichotomous	secund and in all directions	pseudodichotomous (rarely pseudotrichotomous)
Site of reproductive filaments	middle cortex	inner cortex	inner cortex
Apex of carpogonial filaments	hooked	hooked	straight or hooked
Cystocarps	compact	loose	loose

[1] Based on Robins & Kraft (1985).
[2] Based on Kajimura (1994).

Carpogonial and auxiliary-cell filaments generally replace normal cortical filaments in the middle portion of the cortex (Fig. 9). Reproductive filaments rarely arise in the inner cortex, and no filaments were observed borne directly on central-axial cells. Neither type of reproductive filament produces rhizoidal filaments or a thick mucilage coat. Young carpogonial filaments are terminated by a carpogonium that becomes offset following a single oblique division (Figs 10, 11, 14). The second cell below the carpogonium also becomes wedge-shaped, but this is a result of unequal elongation of the cell rather than an oblique division (Fig. 14). Consequently, the filament apex becomes strongly reflexed. Mature carpogonial filaments are composed of 7–11(–14) cells, six to ten of which are modified (rounded, inflated, darkly stained). The mature carpogonium bears a long trichogyne, and the third, fourth, or fifth cells below the carpogonium are usually enlarged and darkly staining (Figs 10, 11).

Auxiliary-cell filaments are composed of 14–33 cells, 8–22 of which are modified (Fig. 12). The generative auxiliary cell is generally smaller than the immediately adjacent cells and occurs centrally in the modified portion of the filament (Fig. 12). A file of unmodified cylindrical cells, often forked, usually terminates the auxiliary-cell filament, and a few of the basal cells may also be unmodified.

After fertilization, the base of the trichogyne becomes plugged and the carpogonium extends into a primary connecting filament (Fig. 15) that fuses with the third and/or fourth cells (nutritive auxiliary cells) below the carpogonium. The resulting fusion complex gives rise to up to six secondary connecting filaments (Figs 16, 17) that traverse long distances to fuse laterally with generative auxiliary cells. The connecting filaments collapse just behind the point of fusion, and the portion of a connecting filament that remains attached to the auxiliary cell inflates somewhat (Fig. 21). This protuberance produces two or three gonimoblast initials that do not recurve around the auxiliary-cell filament (Figs 18, 22).

Mature cystocarps are compact, subspherical, up to 245 μm in diameter, and consist of subspherical, ellipsoidal, or angular carposporangia up to 15–25 μm in length and 8–10 μm in diameter (Figs 20, 23–25). The carposporangial mass does not completely encircle the auxiliary-cell filament but leaves a distinct longitudinal cleft (Figs 24, 25). Simultaneously, the auxiliary-cell filament continues growing and usually reaches the same length as surrounding cortical fascicles. Mature cystocarps are located in the outer cortex, close to the thallus surface (Figs 24, 25).

Tetrasporangia are unknown.

REMARKS: *Dudresnaya canariensis* has no unique features, except the disposition of its spermatangia on elongated mother cells arranged in corymbose terminal and subterminal fascicles, a feature previously unreported in the few species of *Dudresnaya* where male gametophytes are known. *Dudresnaya canariensis* differs from the other fifteen *Dudresnaya* species by a combination of seemingly significant attributes. It differs greatly in habit from the flattened *D. patula*. From *D. bermudensis, D. colombiana, D. georgiana, D. lubrica,* and *D. puertoricensis* it differs in having cylindrical rather than subspherical outer cortical cells. It differs from *D. australis, D. crassa, D. lubrica, D. minima, D. okiensis, D. puertoricensis,* and *D. verticillata* in lacking annulations in the younger branches, and from *D. crassa, D. hawaiiensis,* and *D. japonica* in lacking a thick mucilage coat around reproductive filaments (see tables of characteristics in Robins & Kraft 1985; Kajimura 1993, 1994).

Dudresnaya canariensis seems most closely related to *D. capricornica* from Australia Robins & Kraft (1985) and the recently described *D. kuroshioensis* Kajimura (1994) from Japan. These species show important similarities of overall habit, hexagonal-crystal inclusions, and axis structure. Nevertheless, the new species can be separated reproductively from *D. capricornica* by its corymbose rather than double-whorled spermatangial mother cells, the regularly oblique carpogonial division, gonimoblast initials that do not recurve around the auxiliary cell, and cystocarps that incompletely surround the auxiliary-cell filament to leave a narrow cleft on one side of the carposporangial mass (Table 1). It differs from *D. kuroshioensis* by its considerably thicker rhizoids, the consistent oblique carpogonial divisions, and the noncurving gonimoblast initials (Table 1). *Dudresnaya canariensis* differs also from these two species in relatively minor details: (1) thinner major axes; (2) nonprotuberant, inconspicuous apical cells; (3) the proximal pseudotrichotomies and distal pseudodichotomies of cortical fascicles; (4) the mid-cortical rather than inner-cortical positions of carpogonial and auxiliary-cell filaments; (5) the hooked apices of carpogonial filaments as a result of a single oblique division of the young carpogonium and the unequal elongation of the second cell below it; and (6) the compactly constructed mature cystocarps (Table 1). This combination of differences observed in the Canarian plants appears to justify their description as a closely related but distinct species.

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