# The structure and reproduction of *Dasya haitiana* sp. nov. (Dasyaceae, Rhodophyta) from the Caribbean Sea

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A new species of *Dasya* is described from Haiti (western part of Hispaniola Island) in the Caribbean Sea. The position of successive procarps and the presence of monosiphonous adventitious filaments in *Dasya haitiana* place this new taxon close to the *D. baillouviana* group. It is distinguished from other Caribbean species by the continuing indeterminate growth of the fertile polysiphonous axes once the carpogonia have been fertilized, by the unique formation of adventitious branches, and by its subdichotomous branching pattern.

## INTRODUCTION

The Dasyaceae Kützing (1843, p. 413, as "Dasyeae") was originally separated from the Rhodomelaceae Areschoug (1847, p. 260 as "Rhodomeleae", *vide* Silva 1980, p. 87) and the other families of the Ceramiales Oltmanns (1904, p. 683) by its sympodial growth (Falkenberg 1901; Rosenberg 1933a, 1933b; Kylin 1956; L'Hardy-Halos 1968; Parsons 1975). Rosenberg (1933a, 1933b) made significant contributions in clarifying the Dasyaceae by discovering the pericentral cells of the female fertile segment are cut off in a circular manner, the pericarp is not formed until after fertilization, and that the gonimoblast is monopodially branched (Hommersand 1963). Recently Parsons (1975) added other features to the circumscription of *Dasya* C. Agardh (1824, pp. 34, 211, as "*Dasia*"): the presence of a connecting cell as the means of transferring the diploid nucleus from the carpogonium to the auxiliary cell, and the formation of a fusion cell established by a newly developed connection of the auxiliary cell to the central cell of the fertile segment.

In his classic treatment on the marine algae of the tropical and subtropical American coasts, Taylor (1960, pp. 556–563) included 12 species of *Dasya*: *D. caraibica* Børgesen (1919, p. 319); *D. collinsiana* Howe (1918, p. 524); *D. corym-bifera* J. Agardh (1841, p. 31); *D. crouaniana* J. Agardh (1890, p. 95); *D. harveyi* Ashmead in Harvey (1858, p. 127); *D. mollis* Harvey (1853, p. 62); *D. ocellata* (Grateloup) Harvey in Hooker (1833, p. 335); *D. pedicellata* (C. Agardh) C. Agardh (1824, p. 211); *D. punicea* Meneghini in Zanardini (1842, p. 171); *D. ramosissima* Harvey (1853, p. 61); *D. rigidula* (Kützing) Ardissone (1878, p. 140); and *D. sertularioides* Howe et Taylor (1931, p. 21); and two uncertain records, *D. arbuscula* (Dillwyn) C. Agardh (1828, p. 121), and *D. hussoniana* Montagne (1849, p. 290).

Subsequent to Taylor (1960), several nomenclatural and systematic changes have been made. *Dasya pedicellata,* the type species of the genus (*vide* Farr *et al* 1979, p. 495), has been merged with an older name, *D. baillouviana* (Gmelin) Montagne (1841, p. 164) (see Dixon & Irvine 1970, p. 480). Joly & Oliveira Filho (1966, p. 118) have transferred *D. sertularioides* to *Heterodasya sertularioides* (Howe et Taylor) Joly et Oliveira Filho, a taxon recognized by Parsons (1975) as belonging to the tribe Brongniartellae of the Rhodomelaceae. Dixon (1960, 1964) elucidated the nomenclatural and typification problems of *D. arbuscula* (Dillwyn) C. Agardh resulting in its transfer to *D. hutchinsiae* Harvey in Hooker (1833). The taxonomic position of *D. harveyi* Ashmead remains uncertain (see Harvey 1858; Falkenberg 1901, p. 625; DeToni 1903, p. 1191).

There have been few ecological studies dealing

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with species of *Dasya*. Only one species from the subtropical western Atlantic, *D. baillouviana,* has been studied in the field. Richardson (1981) found that macroscopic plants of *D. baillouviana* from North Carolina appeared in late winter and throughout the spring, and during the remainder of the year it persisted as prostrate discs. Similarly, there have been few chemical studies on the genus. *Dasya baillouviana* var. *stanfordiana* (Farlow) J. Norris et Bucher (1976, p. 19) from the Gulf of California was found to have simple phenols of aromatic structure, which were shown to have antibiotic activity (Fenical & McConnell 1976). These studies suggest that natural product chemistry (Norris & Fenical 1985) and life histories of other species should be investigated for their role in the systematics of *Dasya*.

The marine algae of Haiti (Hispaniola Island) have been recorded by Taylor & Arndt (1929), and Taylor (1933, 1940, 1942, 1960), with new records reported by Norris *et al* (in press). Of all the Caribbean records of *Dasya* species, only one, *D. corymbifera,* has been reported from Haiti (Taylor & Arndt 1929). Herein we describe a second species, thus far known only from Haiti in the Greater Antilles.

## MATERIALS AND METHODS

Procarpic, cystocarpic and tetrasporangial plants, collected by SCUBA diving by M.E. Hay from a back reef lagoon, Caracol Bay, Haiti [21°45′N; 72°00′W], 11 May 1981, were growing as epiphytes on *Acanthophora spicifera* (Vahl) Børgesen and *Thalassia testudinum* Banks ex König. They were preserved in 5% buffered Formalin–seawater solution in the field. Portions of liquid preserved material were stained with aniline blue (Papenfuss 1937) and mounted in Karo syrup on microscope slides (Abbott & Hollenberg 1976). Specimens studied, accompanying microscope slides and liquid preserved portions of #MH-1256 are deposited in the Algal Collection, US National Herbarium, Smithsonian Institution (US). Comparisons of our new species were made

with tropical western Atlantic specimens of *Dasya* (deposited US; determined by W.R. Taylor).

## DIAGNOSIS AND OBSERVATIONS

### *Dasya haitiana* Fredericq et J. Norris sp. nov.

Thallus erectus usque ad 9 cm altae et per hapteron rhizoideum affixus. Axes principales sympodiales 5 cellulis pericentralibus praebentes, ramificatio subdichotoma, ramulis monosiphoniis adventitiis. Procarpia spiraliter in axibus sympodialibus polysiphoniis disposita; axes post fecundationem carpogoniorum crescentes. Cystocarpia sessilia ad maturationem axium, basis proliferatione cellularum corticalium cincta est; cellulae corticales cellulis pericentralibus sub cellula centrale oriundae. Pericarpium partim praecedentis similiter et partim cellulis corticalis cellulis pericentralibus super cellulam centrale formantium ostiolatum; carposporangia pyriformia, ovalia. Stichidia tetrasporangiorum pedicellata lanceolata et leniter curvata in pedicellis monosiphoniis evolutania aut in cellulis pericentralibus sessilia aut in ramulis pseudolateralibus monosiphoniis sessilia. Spermatangia ignota.

Thalli erect, to 9 cm tall, epiphytic, attached by rhizoidal holdfast. Main axes sympodial with five pericentral cells. Branching subdichotomous; with monosiphonous adventitious branches and polysiphonous adventitious branches, the latter originating either from adventitious monosiphonous filaments cut off from pericentral cells or from cortical cells. Procarps spirally arranged on successive segments of unspecialized polysiphonous sympodial axes which continue to elongate after carpogonia are fertilized. Cystocarps sessile, ostiolate, surrounded at the base by a proliferation of cortical cells, with carposporangia pyriform to oval, formed singly on the gonimoblast. Tetrasporangial stichidia stalked or sessile, lanceolate and slightly curved, arising at subdichotomies of monosiphonous filaments, or sessile on polysiphonous axes. Spermatangia not found.

HOLOTYPE: Mark E. Hay, #MH-1256 (#US-93577, including microscope slides #US-3692–3695, and liquid preserved material in vial #5574 of jar #552).

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**Figs 1-4.** *Dasya haitiana* Fredericq et J. Norris, sp. nov.
    **Fig. 1.** Holotype of *Dasya haitiana,* sp. nov. (#MN-1256; #US-35977).
    **Fig. 2.** Adventitious polysiphonous branch (right) and an adventitious monosiphonous branch arising from the pericentral cells (left) (slide #US-3693).
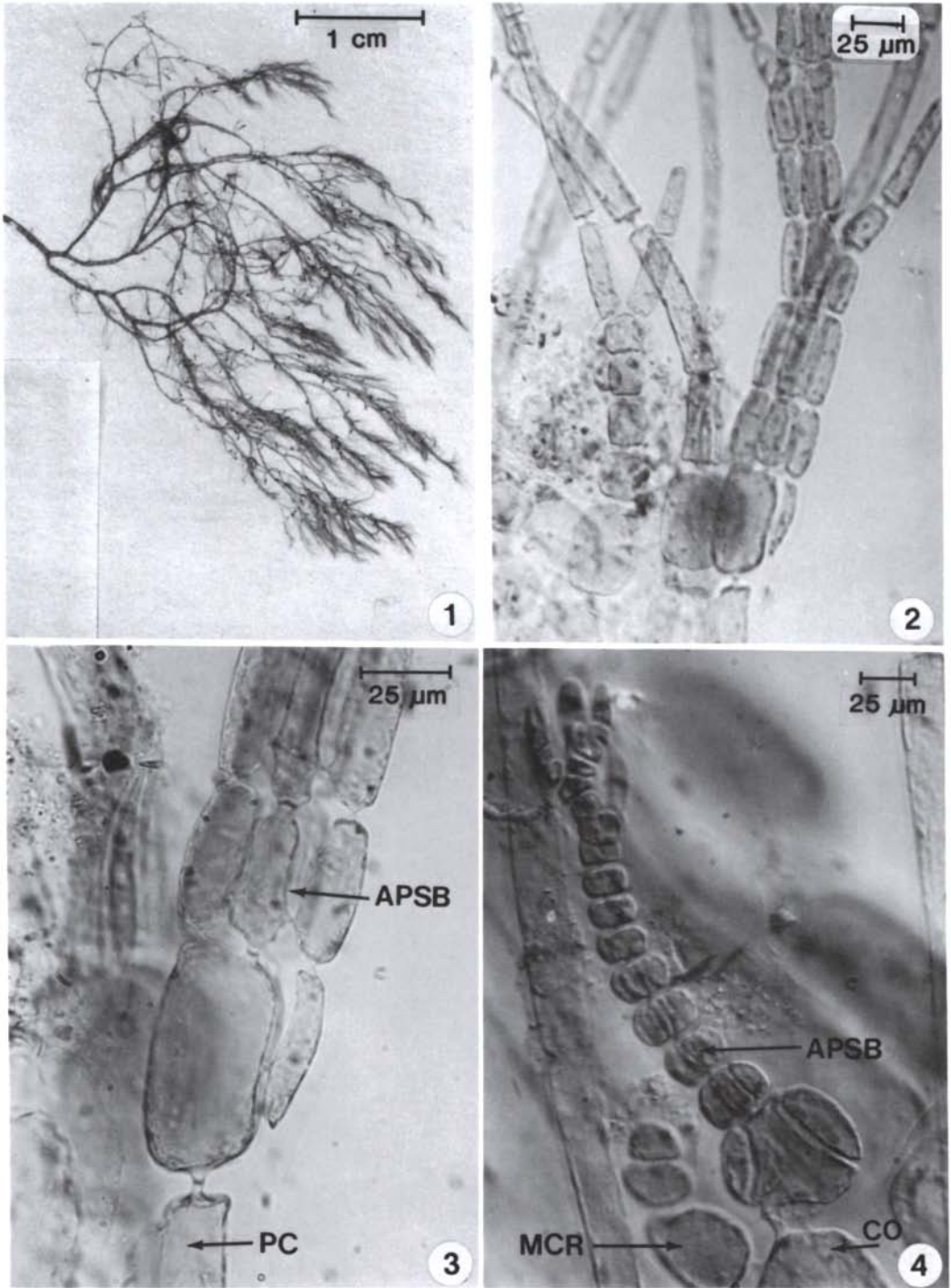
Fig. 3. Adventitious polysiphonous sympodial branch (APSB) arising from a pericentral cell (PC) (slide #US-3693).

Fig. 4. Adventitious polysiphonous sympodial branch (APSB) and a short monosiphonous cell row (MCR) arising from the same cortical cell (CO) (#US-3693).

TYPE LOCALITY: Caracol Bay, Haiti (Hispaniola Island) [21°45'N; 72°00'W].

HABITAT: Epiphytic on *Acanthophora spicifera* (Vahl) Børgesen and *Thalassia testudinum* Banks ex König, 3.0–9.0 m depths, in the *Thalassia* bed of the back reef lagoon.

**Vegetative structure**

A spiral growth pattern characterizes *Dasya haitiana.* The main polysiphonous branches develop from and diverge close to the base, with successive orders of subdichotomous branching and without a percurrent axis (Fig. 1). Adventitious polysiphonous branches, which originate on monosiphonous filaments, and two different types of subdichotomous monosiphonous filaments are also present. One type, the *pseudolateral,* is a monosiphonous filament whose basal cell is pit connected with the main axial cell (e.g. Fig. 2, left). The pseudolateral is formed from the former apical cell as it becomes displaced laterally by a bulge (Fig. 18) on the subapical cell. This bulge on the subapical cell is cut off as a new apical cell taking over the growth of the main axis. The formation of a new non-adventitious polysiphonous branch results from the lower cells of the pseudolateral acting as axial cells by cutting off pericentral cells. Monosiphonous filaments which arise from either pericentral cells or cortical cells and do not influence the direction of the established branching growth are called *adventitious monosiphonous branches* (Fig. 2) (Parsons 1975). In *D. haitiana* one pericentral per segment in a successive spiral manner has the potential to cut off part of its content and form a branch initial which will give rise to an adventitious monosiphonous filament. In some instances the potential branch initial fails to continue to grow into a monosiphonous adventitious filament. However, once these monosiphonous filaments are established, they remain persistent. Adventitious polysiphonous lateral branches can be formed from monosiphonous adventitious fil-

aments becoming polysiphonous in a basipetal direction in its lower segments (Figs 2, 3, 18). The basal segment of the original monosiphonous adventitious filament is shown in Fig. 3. In the lower part of this new polysiphonous branch (Figs 2, 3), the monosiphonous laterals are borne four segments apart. Farther up the branch they are two segments apart, and towards the apices the monosiphonous filaments are one segment apart. Once sympodial growth becomes the established growth pattern, the pseudolaterals are formed on every new segment towards the apex. The polysiphonous adventitious branches do not occur in a regular and predictable pattern throughout the thallus.

The cortical cells first produce an adventitious monosiphonous filament which may become a polysiphonous branch. Cortical cells, though not pit connected to a central axial cell, can also develop adventitious monosiphonous branches (Figs 4, 5). There is a major difference between the development of a non-adventitious polysiphonous axis from a pseudolateral and the formation of an adventitious polysiphonous sympodial branch from an adventitious monosiphonous filament. In the former the distal end of the central cell of the segment carrying the pseudolateral or polysiphonous branch diverges to become part of the new branch (Fig. 2). Whereas in the latter, the central cell of the segment carrying the adventitious branch remains straight (Figs 2b, 3, 18). Monosiphonous adventitious branches are occasionally observed departing from the pericarp. Polysiphonous branches occur frequently at the position of the cystocarp (Fig. 11) and can be interpreted as pseudolaterals of the fertile axis which have secondarily become polysiphonous.

Corticating filaments are present at the first subdichotomy of the leading axis closest to the base. These consist of filaments of oval to rectangular corticating cells cut off by pericentral cells at their lower side, which grow downwards over pericentral cells. A row of cortical cells can extend from its point of origin for a distance of up

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**Figs 5-8.** *Dasya haitiana.*
   **Fig. 5.** Adventitious polysiphonous sympodial branch (APSB) arising from cortical cells (CO) (slide #US-3692).
   **Fig. 6.** Cortical cells (C) cut off from the lower side of a pericentral cell near the base of the main axis (slide #US-3693).
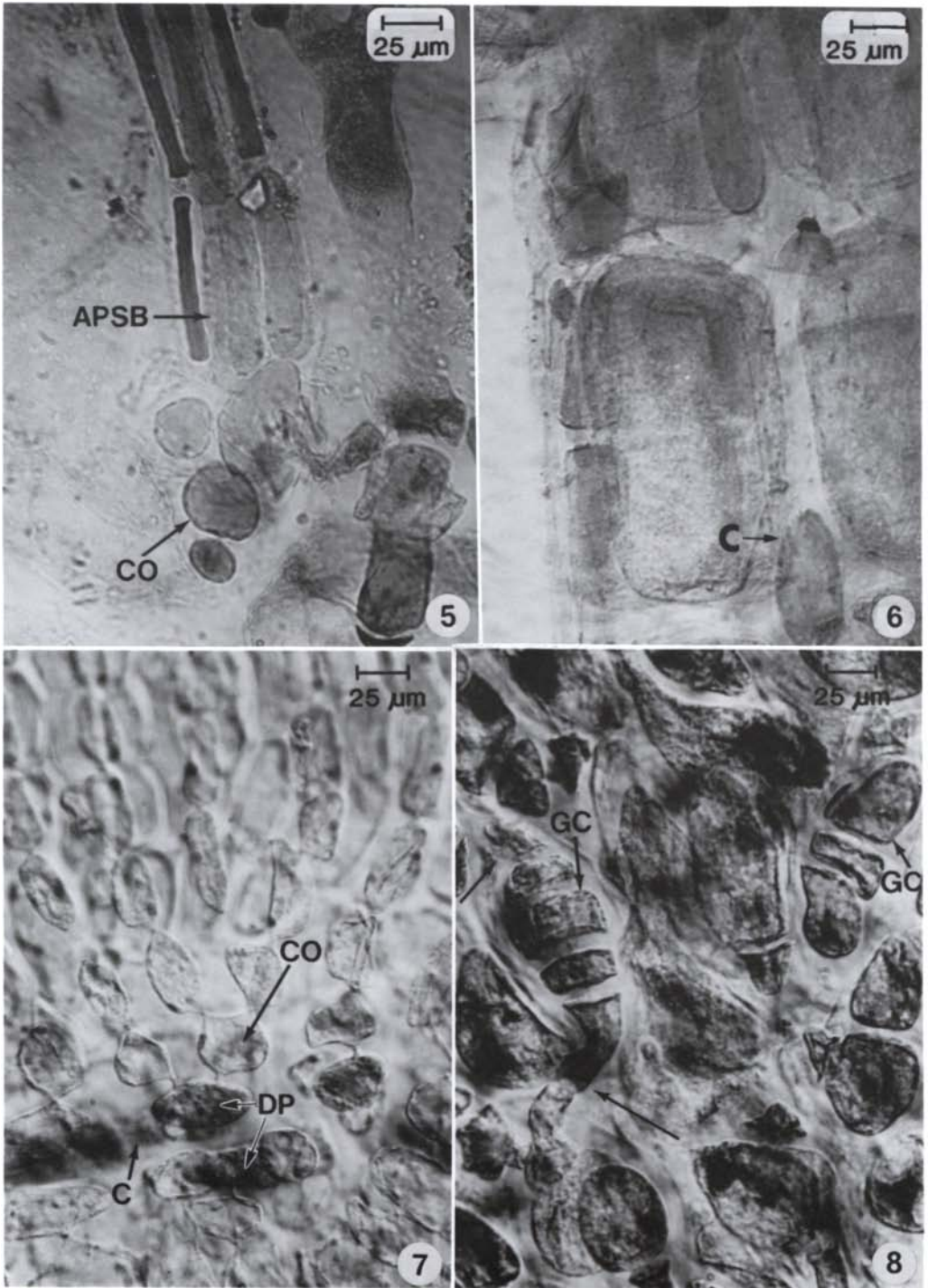
**Fig. 7.** Detail of a pericarp showing linear strings of cortical cells (CO) arising from the dark staining pericentral cells (DP) which lay underneath and above the axial central cell (C) (slide #US-3692).

**Fig. 8.** Mass of germinating carpospores within the pericarp. Note two carpospores in focus (GC), and the bipolar germination pattern (arrows) of the left carpospore (slide #US-3692).
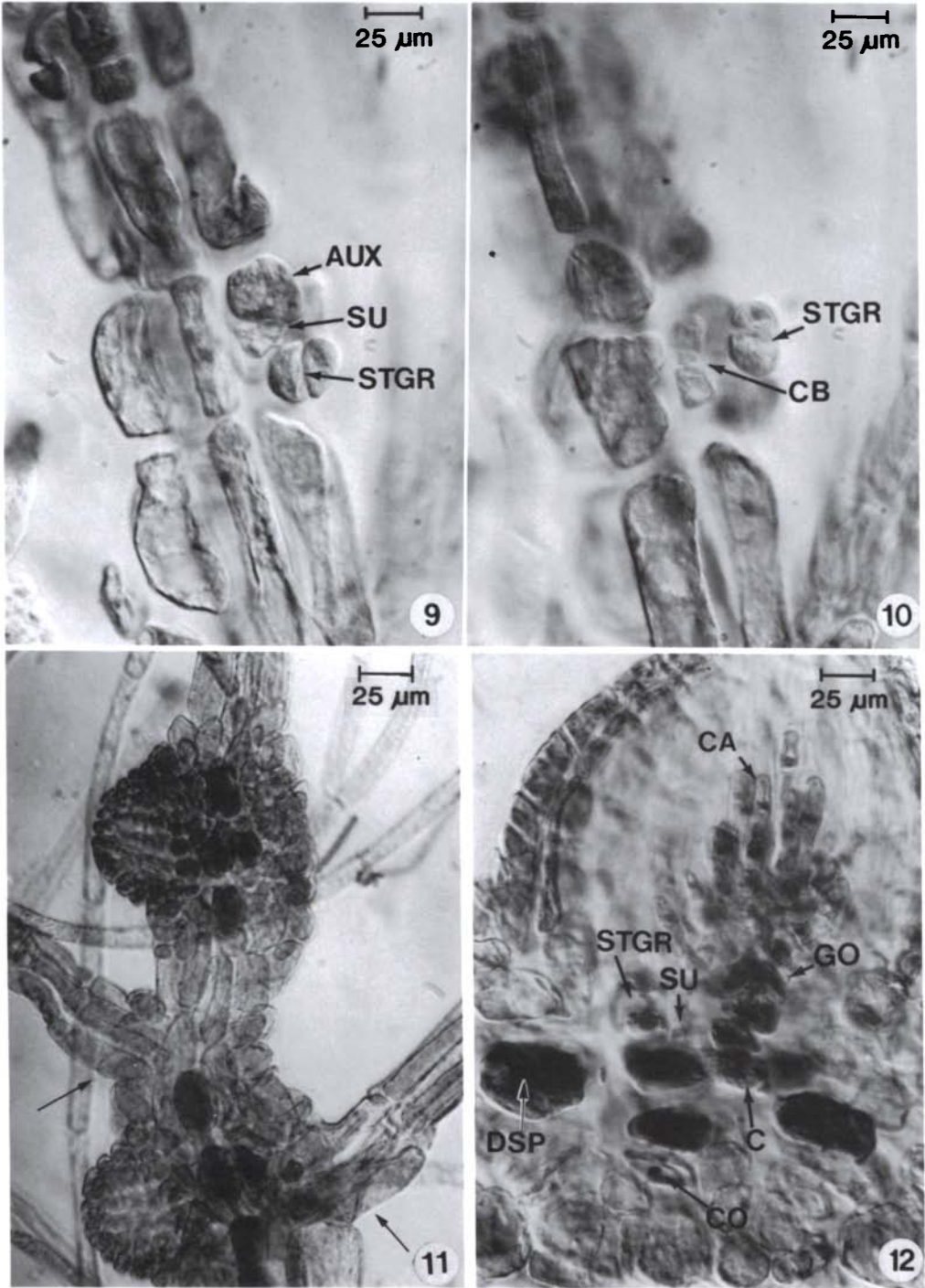
**Figs 9–12.**  *Dasya haitiana.*
   **Figs 9, 10.** The same procarp focused at different depths (slide #US-3692): Fig. 9 shows the auxiliary cell (AUX), and the second group of sterile cells (STGR) in pit-connection to the base of the supporting cell (SU). Figure 10 shows the first formed group of sterile cells attached to the outer side of the supporting cell (STGR), and the carpogonial branch (CB).
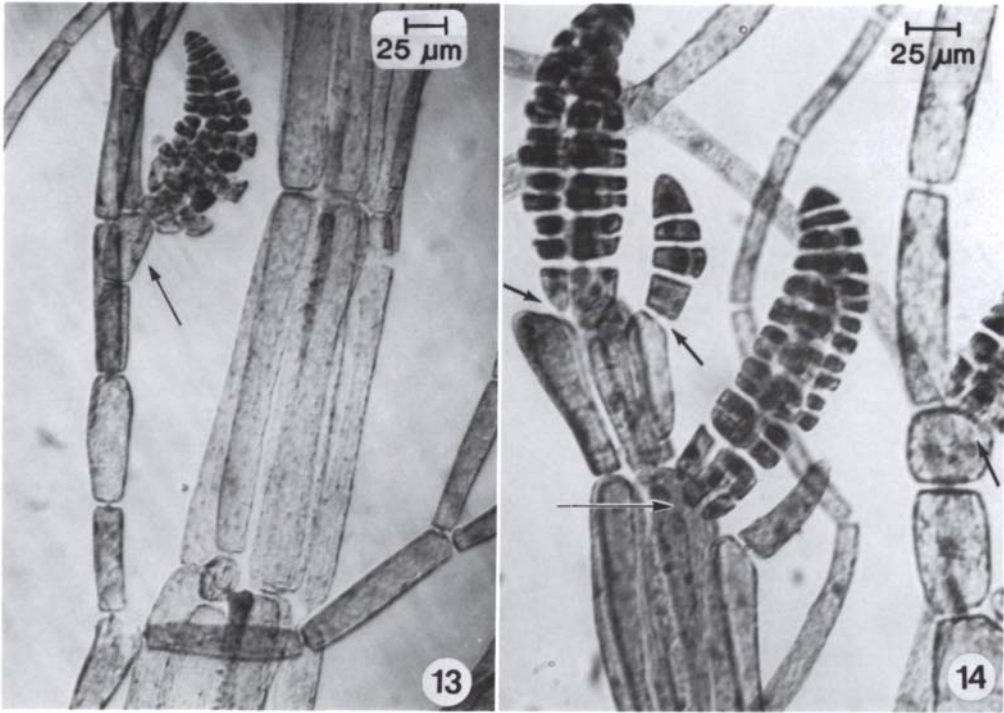
**Figs 13, 14.** *Dasya haitiana.*
    **Fig. 13.** Developing tetrasporangial stichidium borne on a monosiphonous pedicel (arrow) off a monosiphonous filament (slide #US-3694).
    **Fig. 14.** Three immature tetrasporangial stichidia arising directly from pericentral cells (left arrows), and one stichidium which is sessile on a monosiphonous adventitious filament (right arrow) (slide #US-3695).

to eight segments, until they connect to either a pericentral cell or to another cortical cell which was cut off from a different pericentral cell. The cortication sometimes can extend towards the branches (Fig. 6).

**Female reproductive structure**

Procarps are formed, one per segment, successively in a spiral in the upper part of unspecialized polysiphonous sympodial axes (Fig. 15). Sometimes successive segments are sterile. The fertile polysiphonous axes of *D. haitiana* continue to elongate even after several procarps have been fertilized. A fertile pericentral cell divides periclinally, with its inner part becoming the supporting cell and the outer part developing into the first sterile group initial. The supporting cell then cuts off the carpogonial branch initial which develops into a carpogonial branch of 3–4 cells, the last (carpogonium) formed with a prominent trichogyne to 120 $\mu$m long (Fig. 15). After the formation of the carpogonial branch initial, a second sterile group initial is cut off from the supporting cell. Each sterile initial will further divide only once after fertilization. No pericarp initials are formed prior to fertilization. After fertilization, the supporting cell cuts off an auxiliary cell. The actual fusion of the carpogonium

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    **Fig. 11.** Two young cystocarps on a main axis. Note the frequent occurrence of non-adventitious polysiphonous branches (arrows) and the proliferation of cortical cells at the base of the cystocarps (slide #US-3693).
    **Fig. 12.** Mature cystocarp with the central cell (C) bearing the gonimoblast with one gonimolobe in focus (GO), the small supporting cell (SU), and one group of two sterile cells (STGR). The darkly stained pericentral cells (DSP) cut off cortical cells (CO) upwards and downwards to form the pericarp. Note the young elongate carposporangia (CA) developing terminally from the gonimoblast (GO) (slide #US-3693).
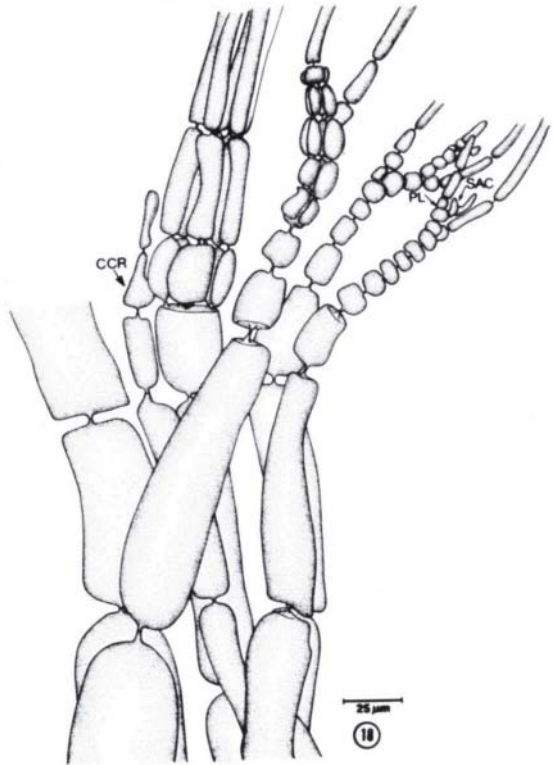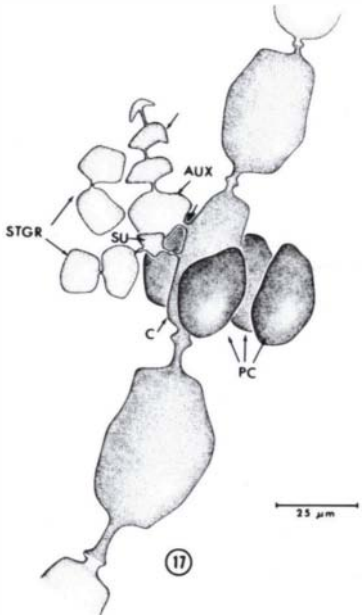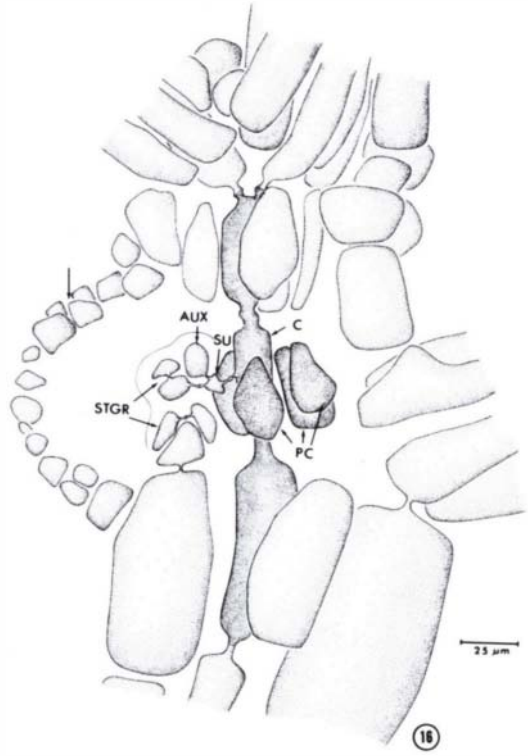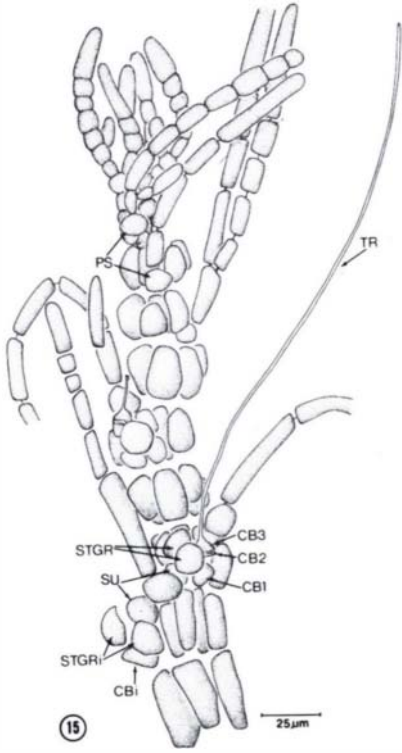
with the auxiliary cell or the formation of connecting cells was not seen, but the developmental sequence of the auxiliary cell and the carpogonial branch was observed (Figs 9, 10). As reported by Parsons (1975) in other species of *Dasya*, the fusion of the auxiliary cell to the central cell of the fertile segment by a new connection to form the fusion cell was also very distinct in our material (Fig. 17). The new connection, although small during the initial stages, becomes larger as the gonimoblast develops.

In young fertilized stages, the supporting cell typically connects to one group of two sterile cells on one side, and to the auxiliary cell on the other side (Figs 9, 10). The first formed group of sterile cells is detached from the supporting cell (possibly due to slide preparation) (Figs 10, 16, 17). In Fig. 17 the pit connection of the supporting cell is clearly seen. The auxiliary cell, after presumed fertilization, divides to produce a primary gonimoblast initial which in turn gives rise to three gonimoblast initials, a terminal one (Fig. 17) followed by two lateral ones. The gonimoblast further develops monopodially, and the carposporangia are formed singly from cells of the branching filaments. Mature carposporangia are pyriform to oval; the elongate carposporangia (Fig. 12) reflect a young carposporophyte.

In every cystocarp of *D. haitiana,* the central cell and remaining pericentral cells of the fertile segment always stain darkly (Figs 7, 11, 12, 16, 17), and could possibly have a nutritive role for the developing gonimoblast (Parsons pers. comm.). The mature cystocarp is sessile, surrounded at the base by a proliferation of cortical cells. Pericentral cells at either side of the fertilized procarp cut off pericarp filaments (Fig. 12) and at the same time the remaining pericentral cells of the fertile segment cut off cortical cells covering the base of the cystocarp. The axial cells of these pericarp filaments cut off pericentral cells which produce cortical cells to the outside of the pericarp (Figs 7, 12). The result is a pericarp formed by several filaments which develop from the pericentral cells lying on either side of the fertile pericentral (Fig. 11).

The very distinct sessile position of the mature cystocarp in *D. haitiana* is unusual in the genus. Also interesting is that the polysiphonous branch bearing the procarps continues to lengthen after fertilization of the carpogonia. In other *Dasya* species, which have their procarps borne on polysiphonous axes, this axis usually stops elongating upon fertilization so that the mature cystocarp appears to be terminal on a polysiphonous stalk (Parsons 1975).

The germination of carpospores with monosiphonous outgrowths extending from both ends of the carpospores was observed within the cystocarp (Fig. 8). Depending on their developmental stage, the non-germinating carpospores can be elongate or elliptical to pyriform, occasionally constricted near the nucleus, and are not uniform in size, but range from 25–50 $\mu$m by 70–110 $\mu$m.

### Tetrasporangial stichidia

Tetrasporangial stichidia are borne at a branch subdichotomy in the pseudolaterals and the monosiphonous filaments (Figs 13, 14). Occasionally they develop from the upper ends of pericentral cells of a polysiphonous axis (Fig. 14), replacing an adventitious monosiphonous filament. The stichidia are sessile (Fig. 14) or borne on a pedicel. Young stichidia are distinguished as a linear arrangement of axial cells which subsequently cut off pericentral cells (Fig. 14).

The mature stichidia are more or less lanceolate and slightly curved, 70–200 $\mu$m wide and

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**Figs 15-18.** *Dasya haitiana.*

**Fig. 15.** Terminal axis showing position of pseudolateral branches (PS) and the location of procarp development sites. Note the carpogonial branch initial (CBi), the carpogonial branch cells (CB$_1$, CB$_2$, CB$_3$) and trichogyne (TR), supporting cells (SU), sterile group initials (STGR$_i$), and sterile cell group (STGR) (slide #US-3693).

**Fig. 16.** Early post-fertilization stage, showing supporting cell (SU) with a group of sterile cells (STRG), the auxiliary cell (AUX), and the pericentral cells (PC). Note that a connection between the auxiliary cell and the fertile central cell (C) has not yet developed, and only a few cortical cells (CO) of the pericarp have been formed (slide #US-3693).

**Fig. 17.** Early post-fertilization stage, showing the supporting cell (SU) with two groups of sterile cells (STGR), the auxiliary cell (AUX) with gonimoblast initials (GO) and the pericentral cells (PC) (slide #US-3693).

**Fig. 18.** Monosiphonous and polysiphonous branches arising from the pericentral cell. Note that the central cell row (CCR) stops its growth. A lateral bulge on the subapical cell (SAC) indicates sympodial growth. A pseudolateral (PL) results from the displacement of the former axial cell (slide #US-3693).

**Table 1.** Comparison of Caribbean *Dasya* species (summarized from Taylor 1960, 1969; Chapman 1963; Oliveira Filho 1969; Oliveira Filho & Braga 1971)

| Species reported | Height (cm) | Main axis diam. (μm) | Branching | Cortication | Pericentral cells L/W ratio | Pericarps | Stichidia pedicel cells |
|---|---|---|---|---|---|---|---|
| *D. baillouviana* (as *D. pedicellata*) | 20–70 | to 260 | sparse to freely alternate | throughout | | stalked urceolate | |
| *D. brasiliensis* | to 15 | <1000 | irregularly alternate | lower | 2–4/1 | | 1 |
| *D. caraibica* | to 20 | | alternate | rhizoidal | | sessile | 1–3; |
| *D. collinsiana* | 1–3 (−5+) | 500–750 | subdichotomous | up to last 2–3 forks | | | sub-sessile or 1 |
| *D. corymbifera* | 5–12 | to 750 | alternate | heavy | (1.5–) 2–3/1 | sessile | 1–3 |
| *D. crouaniana* | 6–6.5 | | subdichotomous | complete | 4/1 | sessile | 1–4 |
| *D. harveyi* | 20–25 | | alternate or secund | dense | | sessile | 1 |
| *D. hutchinsiae* (as *D. arbuscula*) | to 10 | | sparse below; dense above | heavy | 1.5–4/1 | stalked | |
| *D. mollis* | 3–4 | | irregular; or alternate; ±pinnate | complete | 2–3/1 | | sub-sessile to sessile |
| *D. ocellata* | 2–7 | | alternate | heavy | 0.5–1.5/1 | sessile | 1–2 |
| *D. punicea* | 5–10 | | all directions | throughout | | stalked | 1–2 |
| *D. ramosissima* | 15–30 | | repeatedly alternate | mature branches | 5–6/1 | sessile | 1 |
| *D. rigidula* | 2–5 | 300–500 | freely alternate, irregularly dichotomous | ecorticate (except base) | 2/1 | | sessile |
| *D. haitiana* | 5–9 above | 500–600 | subdichotomous | rhizoidal | 2/1 to 16/1 | sessile | sessile or 1–2 |

300–700 μm long. Each pericentral cell in a stichidium divides into a tetrasporangial initial and a stalk cell. The stalk cell cuts off (2–)3 cover cells after the sporangium has been formed. Tetrahedrally divided sporangia result. A stichidium consists of five pericentral cells, with 15 postsporangial cover cells, which cover only a part of the tetrasporangia and are arranged in a whorl. Stalk cells and cover cells are perpendicular to each other and remain pigmented. The tetrasporangia are irregularly spherical, 60–70(–80) μm diam., and mature acropetally within the stichidium. Individual tetraspores can reach 50 μm diam. as seen in surface view.

## DISCUSSION

The features of our new species agree with those of the Dasyaceae as summarized by Parsons (1975), i.e. sympodial growth and the formation of a fusion cell with a new connection of the auxiliary cell to the central cell of the fertile segment. *Dasya haitiana* also agrees well with the generic features of *Dasya*: spirally organized with a sympodial axis with five pericentral cells; procarps arranged spirally on successive axial segments; presence of cortical filaments; monosiphonous, pigmented and persistent pseudolaterals; adventitious monosiphonous filaments arising from pericentral and/or cortical cells; gonimoblast monopodial; tetrasporangial stichidia with five pericentral cells which divide first to form a tetrasporangium and a stalk cell which cuts off (2–)3 post-sporangial cover cells; and cover cells never completely covering the tetrahedrally divided tetrasporangia.

A comparison of some features of our new species with those of other Caribbean species of *Dasya* [as reported in the literature (Table 1)]

reveals that very few have been fully described. *Dasya haitiana* can be easily distinguished by a combination of characters including the continuing growth of indeterminate axes after fertilization of the carpogonial branches, the proliferation of cortical cells around the cystocarp base, the unusual and lax formation of both polysiphonous and monosiphonous adventitious branches, and the subdichotomous branching habit.

The early germination stages of *D. haitiana* carpospores were similar to the early developmental sequence in two species of *Dasya* from Japan (Shirohara & Inoh 1960). Parsons (pers. comm.) suggests that the observed germination within the cystocarps of *D. haitiana* might be abnormal. It might also be an adaptation to the epiphytic existence of *D. haitiana* if the plant is an obligate epiphyte.

Parsons (1975, pp. 597–598) divides the Australian *Dasya* species into two groups based on the presence or absence of adventitious filaments and the position of the successive procarps. Group one includes *D. baillouviana,* and is characterized by the presence of adventitious filaments and with successive procarps spirally arranged on short sympodial axes. In group two, which includes *D. naccarioides* Harvey (see Parsons 1975, p. 598), the monosiphonous filaments are absent and successive procarps are borne alternately on the adaxial surface of the basal segments of a sympodial axis originating from the pseudolateral. *Dasya haitiana,* while possessing the adventitious filaments of Parsons' group one, deviates from this group in that the successive procarps are not arranged on short sympodial axes, but on the main axes. Another unusual feature of *D. haitiana* is that these axes continue to lengthen indeterminately after the procarps have been fertilized. Thus the taxonomic grouping of Caribbean *Dasya* is in need of further study.

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