

Species of Dasyaceae (Rhodophyta) from Hawaii^{1,2}

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ABSTRACT: Eight species of Dasyaceae (Ceramiales, Rhodophyta) are reported from the Hawaiian Islands, extending the geographic range for six of the species into the central North Pacific. The species are *Heterosiphonia crispella*, *Eupogodon anastomosans*, *Eupogodon iridescens*, *Eupogodon pilosus*, *Dasya baillouviana*, *Dasya collinsiana*, *Dasya corymbifera*, and *Dasya iyengarii*. *Heterosiphonia crispella* (as *H. wurdemannii* var. *laxa*) and *D. baillouviana* were previously listed from Hawaii.

TWO SPECIES of the Dasyaceae were among the earliest collections of marine algae from Hawaii (Abbott 1980), but no systematic study of Hawaiian Dasyaceae has been made previously. This study was part of the Master's thesis of the first author (Schlech 1983) and is being put into publication form in anticipation of using this information in a forthcoming marine flora of the Hawaiian Islands. Additional information is provided with respect to a wider distribution range owing to more collections since 1983. The descriptions and comments on species of *Dasya*, except *D. baillouviana*, and all *Eupogodon* species are entirely those of Schlech, as are the descriptions of *Heterosiphonia*. Comments on and interpretations of *Heterosiphonia*, however, and some added distribution ranges were contributed by the second author, who had additional material.

Members of the Dasyaceae are not common in Hawaiian waters and in general collec-

tions it is possible to miss them altogether. A careful examination of subtidal macroalgae will usually yield *Heterosiphonia crispella* (C. Agardh) Wynne, and intertidal mixed turf may show *Dasya collinsiana* Howe, where it may be attached to rock or epiphytically. The most frequently collected taxa, *Eupogodon iridescens* Schlech and *Dasya corymbifera* J. Agardh, are from the shallow subtidal. The remaining species reported here are relatively rare: *Eupogodon pilosus* (Weber van Bosse) Silva, *E. anastomosans* (Weber van Bosse) Silva, *Dasya iyengarii* Børgesen, and *Dasya baillouviana* (Gmelin) Montagne.

The structure that distinguishes the Dasyaceae is the characteristic tetrasporangial branch, a stichidium, which is fusiform to lanceolate, tapering at one or both ends and in which the tetrasporangia mature. Distinctions between some genera, and species in some cases, may be made by the number and shape of the cover cells of the tetrasporangium. These cells are cut off either before the sporangium is initiated (*Heterosiphonia*) or afterwards (*Dasya* and *Eupogodon*), and there may be three (*Heterosiphonia*), two to four (*Dasya*), or two cover cells (*Eupogodon*). Their shapes may be cuboidal to rounded to oval.

An important vegetative feature is the presence or absence of cortication, which are cells, one or two layers thick, that add to the circumference of the axes and branches by forming outside the pericentral cells. In Hawaiian species of *Heterosiphonia* there are no cortications, but many species elsewhere (Par-

¹ We dedicate this paper to the memory of Munenao Kurogi, professor emeritus, Hokkaido University (Sapporo), who died unexpectedly in October 1988. Although known widely as an experimental ecologist, Dr. Kurogi spent many of his later years teaching students the intricacies of systematics, in just the same spirit that the second author is glad to help the first.

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sons 1975) are corticated. In Hawaii, *Dasya* species are corticated, but elsewhere there are some that are not. All *Eupogodon* species are corticated.

The pericentral cells themselves are another important taxonomic feature; their number is thought to be fixed for each species. Following the lead provided by Parsons (1975), attention is given to the pigmented monosiphonous filaments, sometimes called hairs, that are characteristic of Dasyaceae; their angle of branching, shape, and attachment may be helpful taxonomic features.

MATERIALS AND METHODS

Specimens were preserved in 3% formaldehyde-seawater, and permanent microscope slides were prepared using 1% aqueous ani-

line blue, followed by 1% HCl and mounting in a glucose solution. When necessary, small pieces of dried herbarium specimens were soaked using a variety of liquids, none of which was highly successful. For some specimens, the colored monosiphonous filaments that are characteristic of the species were trimmed before slides were made because in some cases they were excessively matted or too numerous and interfered with observation.

Herbarium specimens, which are standard dried specimens, are cited with the major locality first, followed by a specific locality, habitat notes, collector and date if known, and parenthetically where the specimen is. Specimens deposited in the Bishop Museum, Honolulu, are cited BISH; those retained by the authors, as Schlech or Abbott. In the latter case, only microscopic slides have been retained.

KEY TO THE SPECIES OF HAWAIIAN DASYACEAE

1. Thalli less than 1 cm tall; uncorticated; decumbent, filamentous epiphytes on larger algae *Heterosiphonia crispella*
1. Thalli more than 1 cm tall; partly or wholly corticated; erect, saxicolous, rarely epiphytic 2
2. Thalli brownish or black 3
2. Thalli not brown or black; rose, pink, or otherwise 4
3. Thalli brownish, divaricately branched from a small, basal disc; especially dichotomous at apices; monosiphonous filaments long and lax *Eupogodon pilosus*
3. Thalli black, sparingly branched or not branched; monosiphonous filaments usually broken and matted *Eupogodon anastomosans*
4. Thalli iridescent; with a shrublike habit; several axes arising from a thick, trunklike stipe; spirally branched *Eupogodon iridescens*
4. Thalli not iridescent; axes arising from a small, basal disc; alternately, subdichotomously, or irregularly branched 5
5. Thalli forming small hemispherical tufts composed of several unbranched or sparingly branched main axes from a common disc *Dasya iyengarii*
5. Thalli not forming tufts but having percurrent axes, usually from a small basal disc; alternately or subdichotomously branched 6
6. Thalli dark maroon; axis with long, alternately branched laterals; monosiphonous filaments dense and making a silky fringe *Dasya baillowiana*
6. Thalli rosy pink or beige; axis having short laterals with rounded apices; monosiphonous filaments appearing floccose, branching either alternate or subdichotomous 7
7. Axes subdichotomously branched, usually bleached beige or very pale pink, with round, ocellate apices *Dasya collinsiana*
7. Axes alternately branched, deep rosy pink, apices tapering and not ocellate *Dasya corymbifera*

DESCRIPTIONS OF SPECIES

For convenience, species are listed alphabetically within the genus. Localities are listed from north to south within the Hawaiian Islands (Midway in the northwest to Hawaii Island in the southeast) and where practical from the north to the south within each island.

Genus *Dasya**Dasya baillouviana* (Gmelin) Montagne

Figures 1, 2

Montagne, 1841: 164.

BASIONYM: *Fucus baillouviana* S. G. Gmelin, 1768: 165.

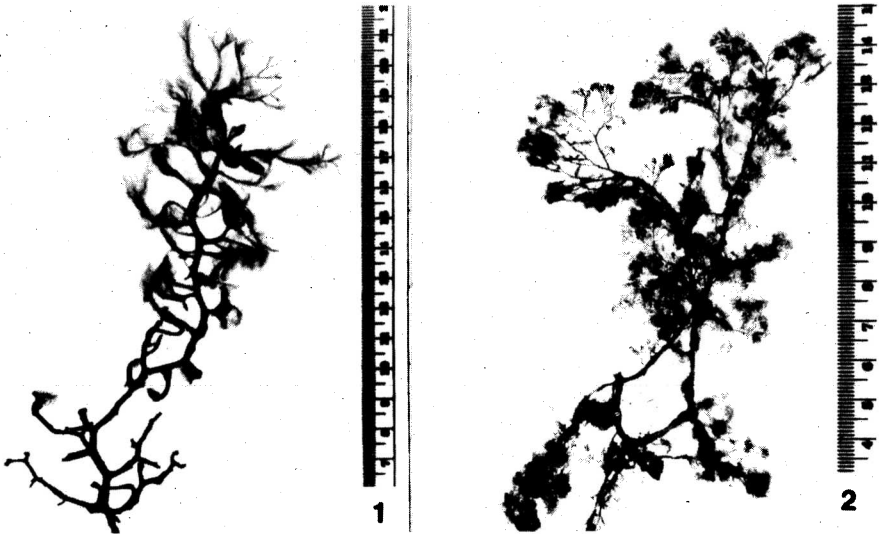
SYNONYMS: *Sphaerococcus pedicellata* C. Agardh, 1822: 321; *Dasya elegans* (Martens) C. Agardh, 1828: 117.

Specimens are between 8 and 17 cm tall with irregular to alternate branching (Figures 1, 2), reddish brown to purplish red on drying. Axes 1 to 2 mm in diameter, branches 0.75 mm at their attachment, tapering at their apices, ulti-

mate branchlets 3–7 mm long. Holdfast absent in material. Main axis with five pericentral cells, densely corticated by a layer of elongated rhizoidal cells 5–8 μm in diameter. Axis and lateral branches clothed with fine monosiphonous filaments that arise spirally from the cortical layer and do not have a distinctive basal cell. They are dichotomously branched once near the base and divided a further three to four times. Monosiphonous filament cells 20 to 55 μm wide by 70 μm long and taper only slightly to their apices.

Tetrasporangial stichidia positioned at the dichotomies, the oldest at the first and younger ones more distal. They have a one- or two-celled pedicel. Stichidia lanceolate to spindle-shaped, somewhat rounded at the base and acute at the apex. Mature stichidia 300–450 μm long and have two cover cells per sporangium.

Spermatangial plants have monosiphonous filaments that are more slender than those on tetrasporangial plants; the linear-lanceolate spermatangial branches are borne in the same positions as tetrasporangial stichidia. Cystocarpic plants were not seen, but cystocarps are described as having a narrow ostiolate neck.



FIGURES 1–2. *Dasya baillouviana*. FIGURE 1. Specimen disengaged from substratum by lobster trap set at 75–90 m depth off Midway Island, Northwest Hawaiian Islands. FIGURE 2. Specimen disengaged from substratum by lobster trap set at 50–60 m depth off Maro Reef, Northwest Hawaiian Islands.

HAWAIIAN COLLECTIONS: Midway Islands, 2 km south of Eastern Island, disengaged from substratum by lobster traps being raised from 75–90 m depth, leg. H. J. Fortner, 1 August 1984 (Abbott 19000, BISH); south side of Maro Reef, disengaged by lobster traps being raised from 50–60 m depth, leg. H. J. Fortner, 14 October 1984 (Abbott 17062, 17464, BISH); northwest side of Maro Reef, disengaged by lobster traps being raised from 50 m depth, leg. H. J. Fortner, 25 November 1984 (Abbott 17346, BISH). Oahu (?), leg. E. Bailey, 1876, BISH 188956; Oahu, J. Rock (no collecting data) (BISH). BISH 190342 was previously cited by Abbott (1980) as constituting one of the earliest records of marine algae from Hawaii.

Descriptions of Pacific material under this name are not uniform, but comparison of the Hawaiian material with specimens of *D. baillouviana* from the Atlantic and Caribbean show a good correspondence. Features such as the cover cells and the position of the stichidia are not mentioned consistently in descriptions and should be investigated in the future. The very fine, slender cortical cells resemble those of *Eupogodon*; other species of *Dasya* tend to have small, rounded cortical cells. The few specimens of *D. baillouviana* examined from the Atlantic and Caribbean, however, show that they, too, have slender cortical cells.

The entangled nomenclature concerning the name of this species (the type species of the genus) is discussed by Dixon and Irvine (1970).

Dasya collinsiana Howe

Figures 3–7
Howe, 1918: 524.

Thalli small and shrublike (Figure 3), often appearing somewhat stoloniferous, forming tufts 1–5 cm tall. A frequent inhabitant of mixed turf and appearing epiphytically; the main axes tend to be spreading, several from a common basal disc 1–2 mm wide, and are percurrent. Living plants are beige with pink, drying to a dingy yellow.

Branches numerous and subdichotomously or irregularly divided seven to eight times

and fastigate in the upper segments. Apices dense and compact, often appearing blunt or rounded (Figure 4).

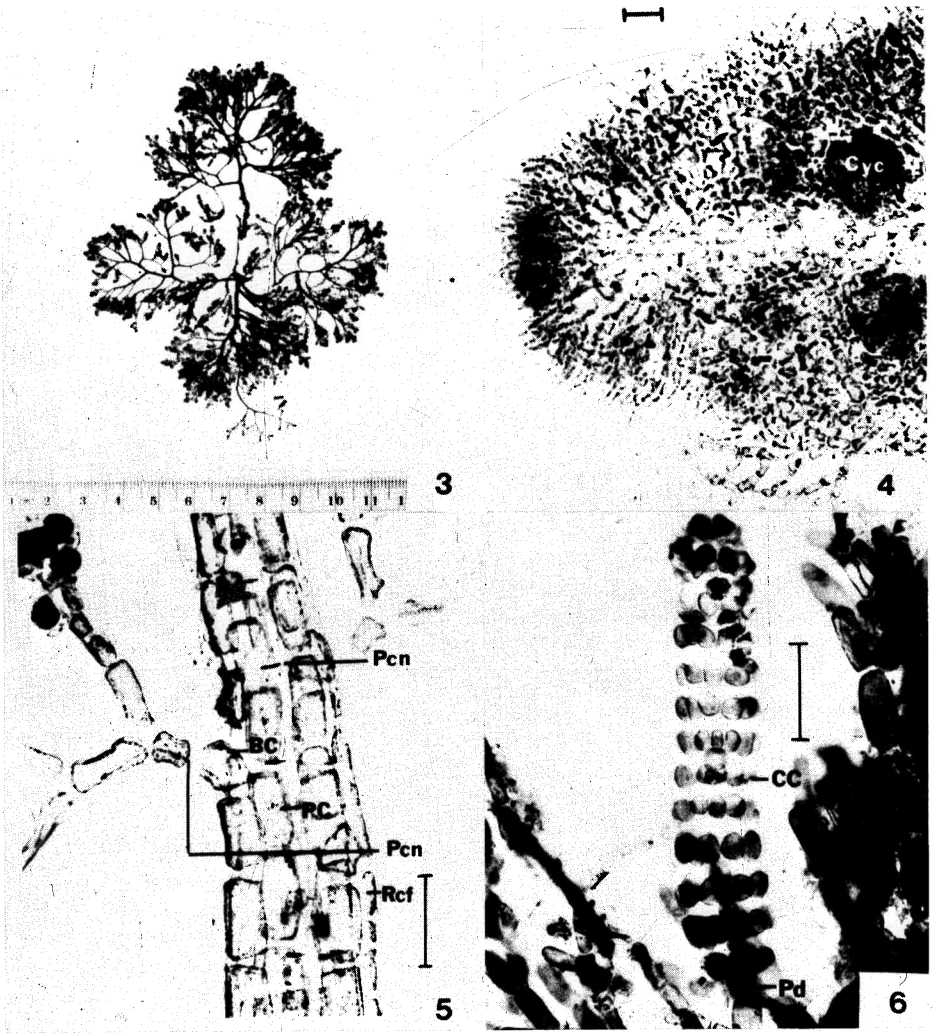
Axes composed of a central filament surrounded by five pericentral cells. The pit connections of the central filament are distinctive, being prominent even in unstained material. The pericentral cells in the upper segments are slightly rectangular, never more than twice as long as wide, but become more cuboidal with age. Those in the lower axial segments range in width between 50 and 70 μm and are 50–100 μm long.

Main axes are completely corticated by cells of variable length and width, cortication beginning with rhizoids from pericentral cells (Figure 5), finally completely covering the main axis, but in the lateral branches cortication is delayed. When old, the corticating cells show a large number of sizes and shapes, and scar cells representing former monosiphonous filaments are also present in those areas.

Monosiphonous pigmented filaments are spirally arranged, one group of filaments to each segment, and derived exogenously from the pericentral cells. They are five to six times dichotomously branched, occasionally more, and the angle of branching is Y-shaped. Filament cell size varies; the basal cells are 30–80 μm wide and 70–150 μm long, and cells toward the tips are usually 10 μm wide. The terminal three to four cells at the tips frequently are sloughed off, resulting in a frayed appearance to the thallus, but additionally giving the appearance of truncated filaments. Sometimes the filaments near the apex stand at some distance from the axis and describe an arching curve, giving an ocellate appearance.

Tetrasporangial thalli are not distinguishable in the field. Stichidia are commonly located on the first dichotomy of the pigmented filaments, sometimes on the second, and are lanceolate when young, becoming more linear when mature. They occur on a one- or two-celled pedicel and are 250–450 μm long when young, reaching lengths up to 600 μm when mature. Three small postsporangial cover cells are formed per sporangium.

Spermatangia of this species are previously undescribed. Spermatangial branches are formed in the same manner as for other species,



FIGURES 3–6. *Dasya collinsiana*. FIGURE 3. Specimen from Molokai. FIGURE 4. Apex of cystocarpic thallus. Cyc = cystocarp. Scale = 100 μ m. FIGURE 5. Early development of cortications showing basal cells (BC), pericentral cells (PC), pit connections (Pcn), and rhizoidal corticating filaments (Rcf). Scale = 100 μ m. FIGURE 6. Mature stichidium showing shape, cover cells (CC) (label is on one of three to the right of the midline), and pedicel (Pd). Scale = 100 μ m.

though spermatangia differ in their extremely small size and thin shape. Spermatangial branch lengths reach 150 μ m and occur on the upper dichotomies of the pigmented filaments, giving a very crowded appearance. Branches (Figure 6) are incurved slightly and develop on a one-celled pedicel, frequently two pedicels being produced by the same bear-

ing cell. Spermatangial branches form dense clusters (Figure 7).

Cystocarpic thalli have similar vegetative morphology. The cystocarps are sessile on determinate lateral branches or main axes but never in the branch axils. They are 500–625 μ m by 800–900 μ m, including the rostrate ostiole, which may occupy 1/3 of the height of

the cystocarp. The pericarp cells are similar to the cortical cells in their irregularity, except around the ostiole where they maintain a catenate orientation. A few carpogonial branches examined showed four cells.

HAWAIIAN COLLECTIONS: Kauai, Lawai Kai, Schlech 235 (BISH). Oahu, Laie Bay, Abbott 34a, 16 March 1941 (BISH); Laie Bay, Abbott 1354, 5 May 1946 (BISH); Kahala Beach, Schlech 226, 234, 238 (BISH); Waikiki, Abbott 332, 12 January 1944 (BISH); Abbott 1091, 8 April 1946 (BISH); Abbott 1138, 19 April 1946 (BISH); Schlech 274–276, 213 (BISH); Ala Moana Beach Park, Schlech 277 (BISH); Ewa Beach (drift), Schlech 200 (BISH); West Beach, leg. F. and M. Tseng (Abbott 18051, BISH). This species is common in turf.

The most distinctive feature at the gross morphological level is the subdichotomous branching pattern and the rounded or blunt branch tips. Additional features that may aid identification in the field are the frequent beige or pale pink color and the small size of this species compared to *D. corymbifera*. Microscopically, *D. collinsiana* may be separated from *D. corymbifera* by its more prominent scar cells, its cuboidal pericentral cells that can be clearly seen even in unstained material that is not yet corticated, and in the less tapered monosiphonous filaments. Spermatangial branches in *D. collinsiana* are less tapered and more compact and more numerous. Cystocarps differ in their placement in *D. corymbifera* by being borne in a branch axil instead of directly on a lateral as in *D. collinsiana*.

Dasya corymbifera J. Agardh

Figures 8–10

J. Agardh, 1841:31.

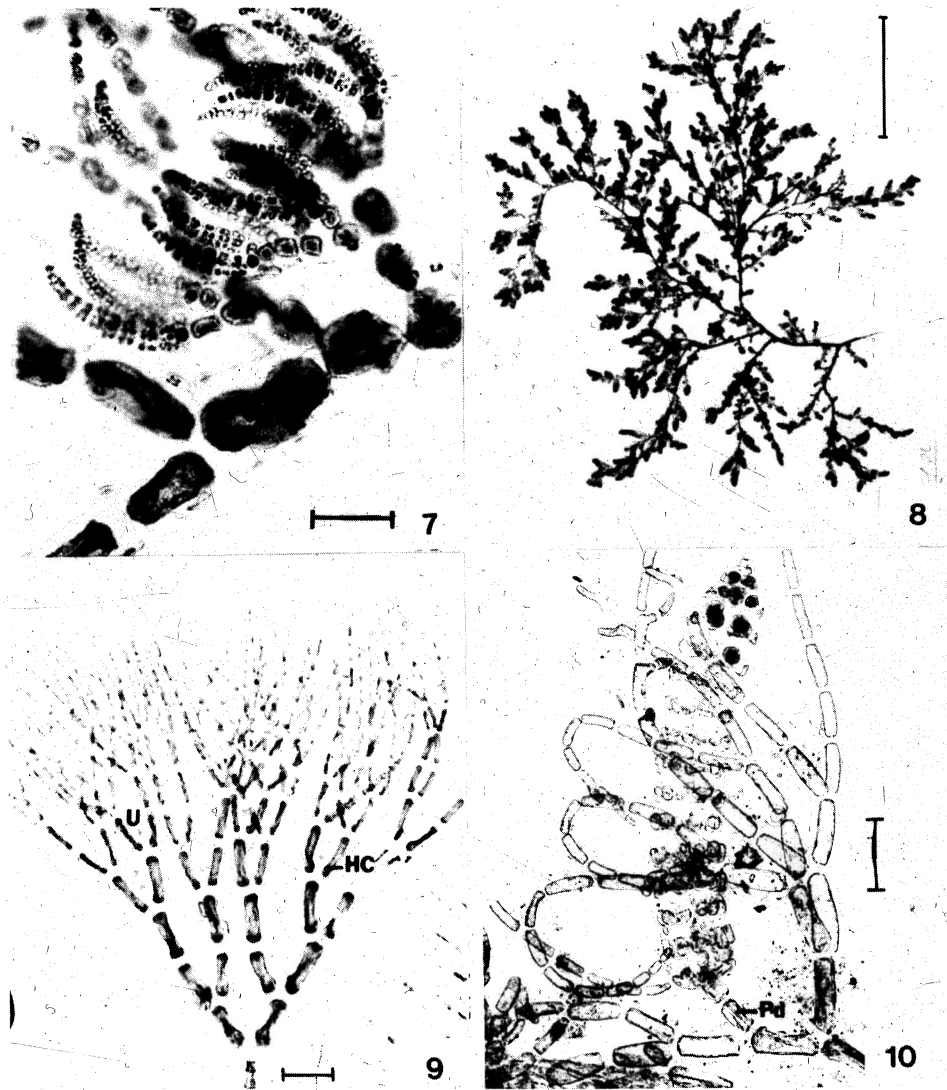
Thalli are up to 15 cm tall, although most are between 7 and 10 cm, and have a soft, flexible habit (Figure 8). Plants are often pyramidal in outline with shorter branches at the base, and when living, have a deep rose color, drying to a bright magenta or brownish red. Apices are often ragged in appearance, as the younger monosiphonous filaments are strongly incurved initially, becoming less so with age.

Main axes lightly to entirely corticated, depending on age, by small, thin and irregular rhizoidal cells, in this way resembling the cortex of *D. baillouviana*. Cross sections near the apex reveal a central filament surrounded by five pericentral cells and a cortical layer. Mature pericentral cells may reach a length of 200 μm or more. Axes secondarily bilaterally organized and alternately branched, although in some cases two branches may occur on the same side successively.

Branches and upper segments of axes covered with spirally and loosely arranged monosiphonous pigmented filaments, one to each segment. Filaments are derived from a roughly isodiametric basal cell 40–50 μm wide, which originates exogenously from a pericentral cell. They become deciduous in older segments, and location of the basal cell is marked by a scar cell. Filaments (Figure 9) are dichotomously branched at least four to five times, sometimes more, and the dichotomy is of the Y-shaped type; filaments somewhat incurved, tapering, and extremely fine at the tips. The cells vary in size but most are 40–60 μm in diameter and 70–90 μm long, becoming smaller toward the tips, the terminal cell of which is about 10 μm in diameter and acutely pointed.

Tetrasporangial thalli are not distinguishable in the field. Stichidia are formed at the second or third dichotomy of the hair and, rarely, there may be more than one on a single hair tuft. Stichidia are subtended by a one- to two-celled pedicel, the latter occurring more commonly. Stichidial shape varies frequently; immature stichidia are conical-lanceolate and become linear (Figure 10) with age. Mature stichidia also exhibit a flattening of the tapered tip. Most stichidia bear a three- to four-celled sterile terminal filament. Three postsporangial cover cells are formed per sporangium, covering about 1/4 of the sporangial height. These cover cells become flattened and more rectangular with age, but always maintain a loosely banded appearance (Figure 10). Overall stichidial length ranges from 400 to 650 μm when fully mature.

Spermatangial branches are formed in the same manner as tetrasporangial stichidia except that the fertile pericentral cells each divides



FIGURES 7-10. FIGURE 7. *Dasya collinsiana*. Immature spermatangial branches showing clustering and pedicels. Scale = 100 μ m. FIGURES 8-10. *Dasya corymbifera*. FIGURE 8. Habit of specimen from Keehi Lagoon, Oahu. Scale = 2 cm. FIGURE 9. Branched monosiphonous pigmented filament (HC) showing attenuate terminal filaments, and Y-shaped angle of branching (U). Scale = 100 μ m. FIGURE 10. Mature stichidia showing shape, incurved "protective" filaments and two-celled pedicel (Pd). Scale = 100 μ m.

to form two spermatangial mother cells. Each mother cell cuts off two spermatangia, which are club-shaped, the flattened end being the terminal one. Spermatangial branches have a one-celled pedicel and are formed on the ultimate dichotomies of the filaments. Occasion-

ally both dichotomies will form spermatangial branches, but they are never clustered.

Cystocarps reach a width of 500 μ m and a length of 985 μ m. They occur in the axils of the determinate lateral branches and are sessile. The pericarp is composed of irregular cells

and mature cystocarps have a beaked ostiole, the diameter of which is consistently smaller than that of the pericarp.

HAWAIIAN COLLECTIONS: *Dasya corymbifera* is the most frequently collected species of *Dasya* in Hawaii. Its distribution is wide (from 28° N to 21° N), although its habitat is strictly subtidal. Thalli grow under a wide variety of epiphytic and saxicolous conditions, but are most commonly collected as drift material.

Midway Islands, Sand Island, 10–50 m off-shore of Picket Pt., on sand and coral rubble, 1–3 m depth, leg. H. J. Fortner, 29 June 1983 (Abbott 17504, BISH). Oahu, Waikiki, Abbott 349, 12 January 1944 (BISH); on Natatorium wall, leg. Jane Lewis, 31 March 1984 (Abbott 18377, BISH); same place, Schlech 212, 229, 232, 257, 276a (BISH); Keehi Lagoon near islet off reef runway, leg. Erika Wyrski, October 1978 (Abbott 14543, BISH); Ewa Beach (drift), Abbott 15631, 22 November 1979 (BISH); Schlech 219–223, 245–257, 299 (BISH); Fort Kamehameha (drift), Schlech 236 (BISH); Barber's Point, on eroded coral benches exposed at –0.1-ft tide level (Abbott 18043, BISH); West Beach, intertidal, leg. F. and M. Tseng, 1 March 1987 (Abbott 18053, BISH). Maui, Launiupoko State Park (drift), 30 August 1977 (Abbott 13119, BISH); 25 July 1984 (Abbott 17428, BISH); Hana, Kauiki Head, subtidal 2–3 m depth, leg. D. P. Abbott, 26 August 1976 (Abbott 14578, BISH); Hokuula, on basalt rock, leg. D. P. and I. A. Abbott, 26 August 1976 (Abbott 14617, BISH). Hawaii Island, Keahole Point, 10 m depth on rope core sample, leg. E. A. Kay, Fall 1981 (Abbott 16055, BISH); Anaehoomalu Bay, ca. 15 m depth, M. Foster, 1 May 1988 (Abbott 18732, BISH).

The Hawaiian specimens and the above description of them agree well with the species as known from the Caribbean (Børgesen 1915–1920, Taylor 1960) and Bermuda (Collins and Hervey 1917, Howe 1918). However, size and branching characteristics shown by *D. corymbifera* allow separation from other tropical species of *Dasya*, such as *D. collinsiana* and *D. carabaica* Børgesen. It differs from *D. carabaica* in its smaller size and lack of ocellate tips

and from *D. collinsiana* in its larger size and more tapered tips. As the species is defined in this paper, monosiphonous pigmented filament groups are shorter, the cells larger, and the filaments more angular in *D. collinsiana*. Hair clusters in *D. corymbifera* tend to taper more than they do in *D. collinsiana*. Y-shaped dichotomies in the monosiphonous filaments are seen in *D. collinsiana*, *D. corymbifera*, and *D. baillouviana*.

Schlech has selected no. 44053 in the Agardh Herbarium, Botanical Museum, Lund University, as the lectotype specimen for this species, inasmuch as no specimen has previously been named as the holotype. Unfortunately, the specimen is not reproductive, but all vegetative characteristics agree well with subsequent material identified with this species. The lectotype material was collected by P. K. A. Schousboe.

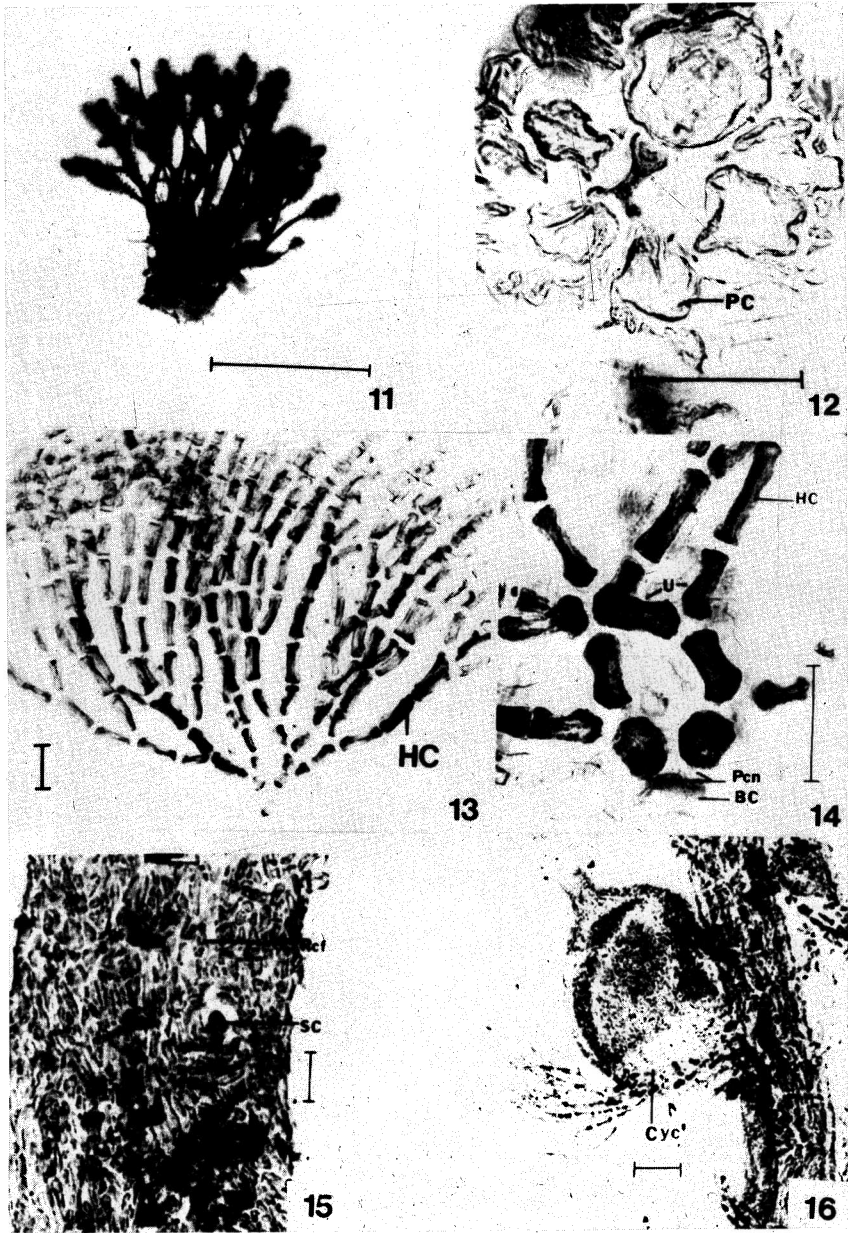
Dasya iyengarii Børgesen

Figures 11–16
Børgesen, 1937: 345.

Thalli small, forming hemispherical tufts (Figure 11) 1–2 cm tall, dark reddish purple when living, drying to deep brownish red. Cushions are composed of several main axes from a 1- to 1.5-mm basal disc, some of them spirally branched once or twice. Branches taper toward tips and younger portions of axes are entirely clothed with filaments that are particularly dense at apices, giving them a rounded, obtuse shape.

Cross sections show five pericentral cells (Figure 12) surrounded by a well-developed single layer of cortical cells. Pericentral cells are rectangular when young, becoming square with age, about 120 by 170 μm when mature. Cortication begins between the pericentral cells with small, irregular to cuboidal rhizoidal corticating filaments that are about 10 μm wide and 40 μm long. The mature axis is entirely corticated although the primary pit connections of the central axial filament may be seen through the cortex.

Monosiphonous pigmented filaments are derived exogenously from the hair basal cell, and are spirally arranged, one to each seg-



FIGURES 11–16. *Dasya iyengarii*. FIGURE 11. Habit of thallus from Kauai. Scale = 1 cm. FIGURE 12. Cross section of mature axis showing five pericentral cells (PC). Scale = 100 μ m. FIGURE 13. Branched monosiphonous filaments (HC), showing relatively nontapering terminal portions and Y-shaped angle of branching. Scale = 100 μ m. FIGURE 14. Detail of Y-shaped angle of branching (U). BC = basal cell, HC = monosiphonous filament; Pcn = pit connection. Scale = 100 μ m. FIGURE 15. Mature cortex showing scar cells (SC), and corticating rhizoids (Rcf). Scale = 100 μ m. FIGURE 16. Mature cystocarp (Cyc) showing sessile position on the axis and its rounded shape. Scale = 100 μ m.

ment, moderately incurved and subdichotomously divided four to five times (Figure 13). The angle of branching (Figure 14) is the Y-shape type. Filaments taper slightly toward the tips. The distinctive feature of the filaments in this species is the presence of two pit connections distally from the basal cell to two different cells; technically, there are two filaments per basal cell, instead of one as seen in *D. corymbifera* and *D. collinsiana*. The more crowded filaments give the impression of whorls at the nodes. The basal cell remains after the filaments become deciduous, forming a scar cell (Figure 15) about 40 μm wide and 50–60 μm long. Monosiphonous filament cells range in width between 10 and 15 μm , up to 100 μm long, and have rounded end walls. Tip cells are about 6 μm wide and 10–20 μm long.

Tetrasporangial plants are not distinguishable in the field. Stichidial sizes vary up to 300 μm and are oblong-lanceolate when young and lanceolate when mature. There are three cover cells per sporangium, and stichidia are positioned on a one- or two-celled pedicel that arises from the first dichotomy of the hair.

Spermatangial plants are previously undescribed. Spermatangial branches are formed at the base of a branched filament, in clusters of sometimes as many as six branches. The branches are strongly incurved and often topped by a sterile portion; lengths range between 150 and 200 μm .

Cystocarpic plants are previously undescribed. The cystocarps are sessile (Figure 16); the carpogonial branch develops at about the fourth segment from the apex. The pericarp is continuous, forming a flask-shaped body with an ostiole at the top, with an overall spherical-globose shape. Cystocarp size ranges between 600 and 750 μm in diameter and 1.0 to 1.5 mm in length.

HAWAIIAN COLLECTIONS: Open coast, wave-washed reefs form the habitat for this species. Kauai, on rock at Lawai Kai, Schlech 264, 265, 273, 283 (BISH), Abbott 15808, leg. Gordon Daida, 8–9 September 1979 (BISH); Kipukai, Schlech 261, 298 (BISH); Oahu, Kaloko, on *Cladophoropsis* sp., leg. I. Abbott & R. E. Norris, 2 September 1961, Abbott 14869 (Abbott); Hawaii Island, Richardson's Bay,

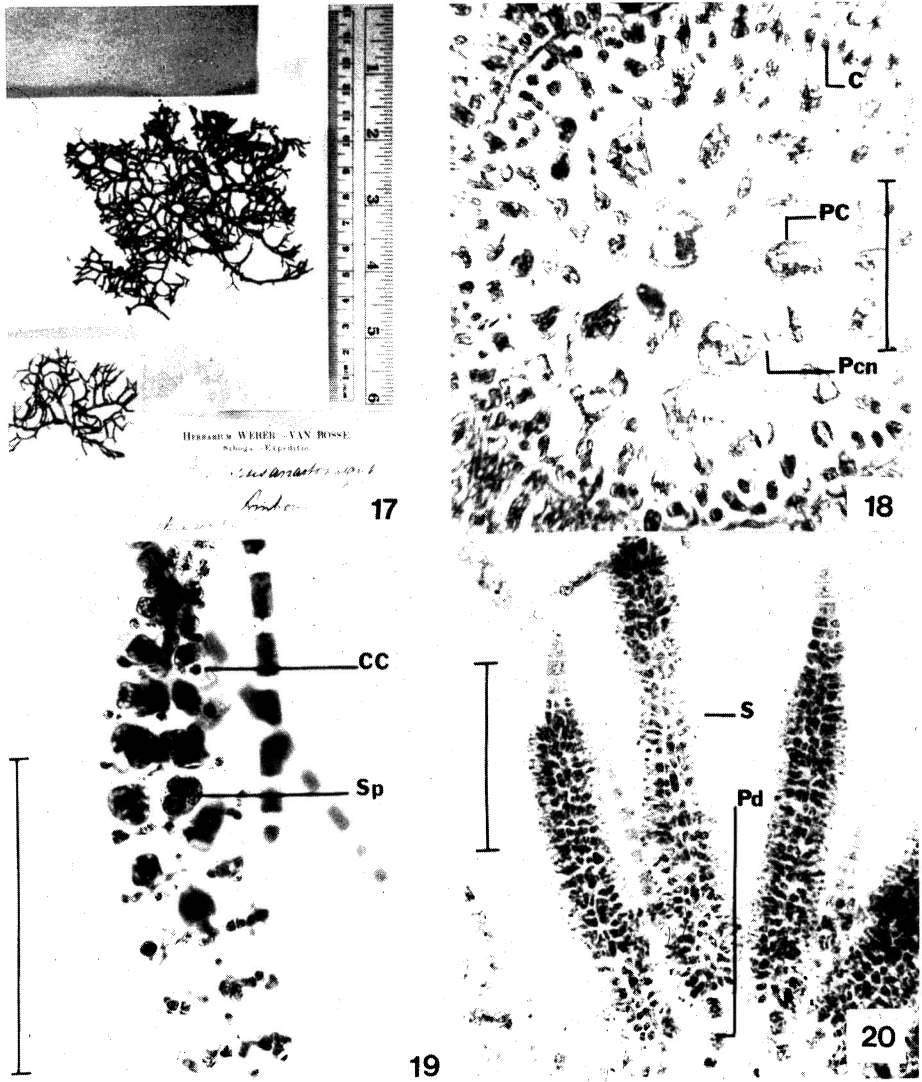
Schlech 204 (BISH). *Dasya iyengarii* is not a common species in Hawaii.

Originally described as epiphytic, *D. iyengarii* has been collected epiphytically and on rock in Hawaii. The specimens agree with previous descriptions (Børgesen 1937, Dawson 1957) except that the cortex appears to be more developed in Hawaiian material. This may be merely an environmental adaptation to a more active habitat zone. Additionally, the monosiphonous filaments are not as strongly incurved as shown for the type specimen by Børgesen (1937, fig. 346).

This species may be distinguished from other *Dasya* in the field by its tufted habit and smaller size. Although it does not resemble *Dasya collinsiana* in any way at the gross morphological level, microscopic examination clouds the distinctions and the two species are similar in many features. However, closer inspection reveals the two filaments per basal cell in *D. iyengarii* compared to one filament per basal cell in *D. collinsiana* and *D. corymbifera*. The crowded appearance of spermatangial branches is undoubtedly connected to the number of filaments on each basal cell, and in this feature it is different from other Hawaiian *Dasya* species.

Genus *Eupogodon*

Species in this genus were formerly placed with the genus *Dasyopsis*, which is a later homonym of *Eupogodon* as interpreted by Silva (1987). The species are separated from *Dasya* vegetatively on the basis of their bilateral organization, as opposed to the radial organization of species of *Dasya*, but there are some exceptions here as in other characteristics. Species of *Eupogodon* treated here also have a distinctive subcortical layer, a "medulla." This kind of tissue has been previously described as pseudoparenchymatous by Parsons (1975) and is formed by extensions of the lower edges of the pericentral cells (Parsons, pers. comm.). This layer occurs between the pericentral cells and the cortex. *Eupogodon anastomosans* and *E. pilosus* show two and *E. iridescens* shows three cover cells per sporangium; Hawaiian *Dasya* show three cover cells



FIGURES 17-20. *Eupogodon anastomosans*. FIGURE 17. Type specimen from New Guinea (Leiden herbarium). FIGURE 18. Transverse section of a mature axis showing pit connections (Pcn), pericentral cells (PC), and cortex (C). The tissue between the pericentral cells and the cortex (the medulla) is present in *Eupogodon* and lacking in *Dasya*. Scale = 100 μ m. FIGURE 19. Mature stichidium showing sporangia (Sp) and very small cover cells (CC). Scale = 100 μ m. FIGURE 20. Spermatangial branches with spermatangia (S), and showing two-celled pedicel (Pd). Scale = 100 μ m.

per sporangium. The observations of two cover cells for *Eupogodon* are in conflict with the conditions found in the type species by Kylin (1956), who stated that there are three cover cells in *Eupogodon* (as *Dasyopsis*). It is clear that further critical studies of the features of these taxa are needed.

Eupogodon anastomosans (Weber van Bosse)
Silva

Figures 17-20
Silva, 1987: 129.

BASIONYM: *Dasyopsis anastomosans* Weber
van Bosse, 1921: 309.

Thalli (Figure 17) small, mostly between 2 and 3 cm tall, very dark red to blackish, margins of branches conspicuously marked by long, matted filaments. Main axes often unbranched or, if branched, only slightly and irregularly so, branches tapering toward tips. Axes covered with a thick layer of fine, matted hairs that are not curved or stiff and are most dense at the apices, being deciduous at the base. Hair cells vary in size and can be roughly twice as long as wide (15 by 15–40 μm) and square, becoming somewhat longer with age. Overall length of the monosiphonous pigmented filaments is about 1–2 mm; they are rarely subdichotomously branched once at the base. They are derived exogenously from a rounded cortical cell; most other cortical cells are thin and slightly elongated.

Main axes, which are sometimes indistinct in branched thalli, are erect and entirely corticated. Cross sections of the major axis reveal a central axis surrounded by five pericentral cells. Exterior to the pericentral cell layer is a medullary region (Figure 18) composed of smaller, parenchyma-like cells, decreasing in size toward the cortex. The cortex is one cell thick and the cells are small and darkly pigmented. The pseudoparenchymatous medulla develops quickly, making recognition of the pericentral cells difficult in mature sections.

Tetrasporangial thalli are not distinguishable from sterile thalli in the field. Lanceolate stichidia are formed on a two- to three-celled pedicel and are formed at the first dichotomy of the monosiphonous filaments; each sporangium is subtended by two postsporangial cover cells that do not cover any portion of the sporangium (Figure 19). Stichidia average about 200 μm in length but may become larger with age. Stichidial cells are loosely arranged compared with the more densely compacted arrangement of stichidial cells in other species and additionally have an unusually thick layer of gelatinous material.

Spermatangial branches are formed in the same manner as tetrasporangial stichidia and reach lengths of 300 μm , although most are between 250 and 260 μm , not including the one- to four-celled pedicel. Spermatangial branches (Figure 20) may occur in clusters of two or three per filament. Spermatangial cells

are slightly teardrop shaped and are attached at the pointed end.

Female plants were not collected and remain undescribed for this species.

HAWAIIAN COLLECTIONS: Hawaii Island, Shipman ranch on intertidal bench, leg. W. H. Magruder 243 (BISH); Richardson Beach Park on basalt boulders, Schlech 205 (BISH). The plants were exposed to strong wave activity. They grow as distinctive isolated plants in a ring.

Because only two collections have been made, the documentation of this species in Hawaii should be viewed tentatively. Moreover, the material matches rather well the descriptions of *Dasya adhaerens* Yamada from the western Caroline Islands (Yamada 1944), which was further described by Taylor (1950) from Bikini atoll. Unfortunately, the type material of *Dasya adhaerens* cannot be located at this time. Should it or other type material become available, a comparison with *Eupogodon anastomosans* should be made. If they represent the same taxon, the epithet *E. anastomosans* should be used, as it has priority. Moreover, the anatomy shows that a subcortical layer makes the placement in *Eupogodon* correct.

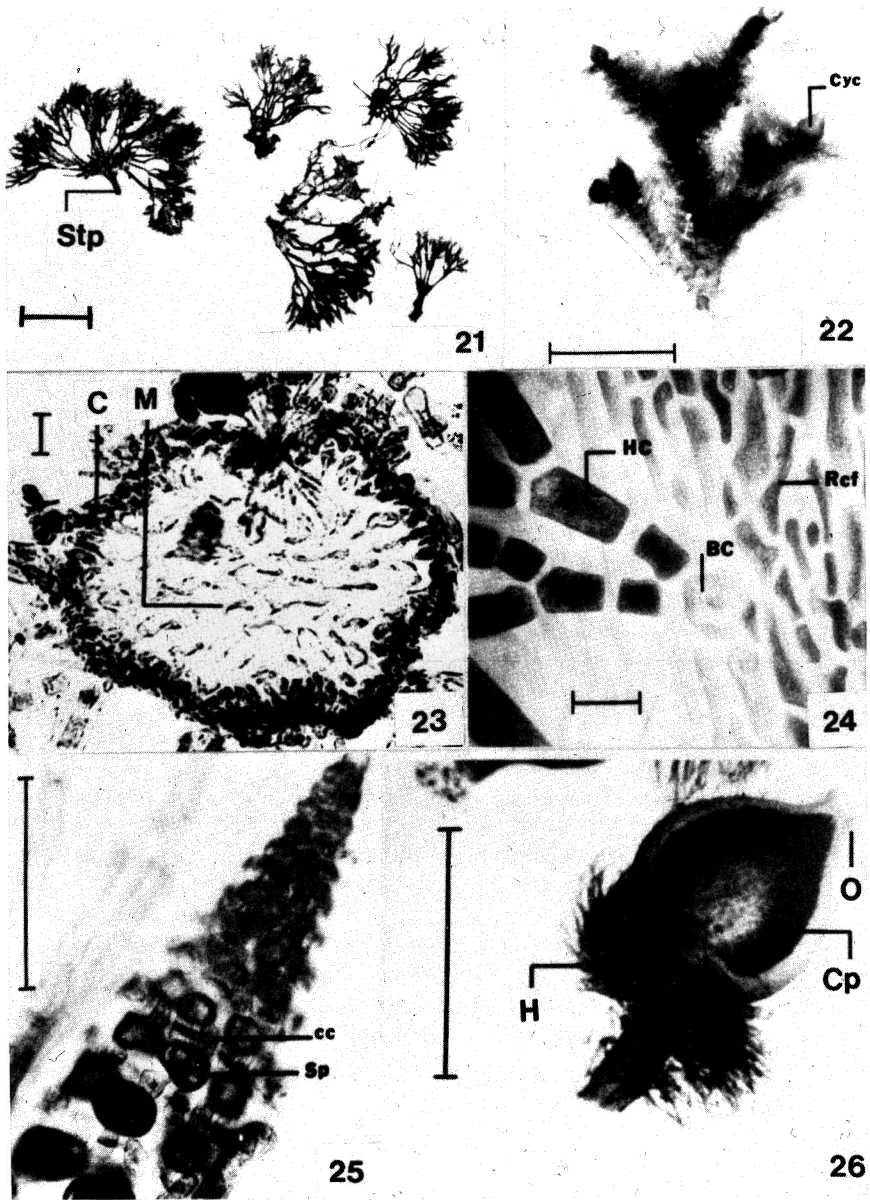
Eupogodon iridescens Schlech

Figures 21–26
Schlech, 1989 (in press)

Plants (Figure 21) reach 7 cm in height and have a distinct iridescence when living, drying to rusty red or bright orange. Several major branched axes are borne on a thick, erect stipe. Major axes are up to 3 mm in diameter, emerging radially near the top of the stipe and are terete and irregularly spirally branched. Stipe narrows basally into a thick, cartilaginous, and sometimes branched holdfast.

Branches, which may be 2 cm or more long, taper toward tips and are clothed with tufts of monosiphonous filaments (Figure 22) that arise exogenously and randomly from the cortex. Filaments are deciduous with age and the bottom halves of the branches become bare.

Cross sections close to the apex (5 mm) reveal a central cell surrounded by several to eight or more pericentral cells and a cortical



FIGURES 21–26. *Eupogodon iridescens*. FIGURE 21. Holotype, Schlech 300 from Punaluu, Oahu, Hawaii (Bishop Museum). Scale = 2 cm. Stp = stipe. FIGURE 22. Branch habit of female gametophyte showing terminal cystocarps (Cyc). Scale = 1 cm. FIGURE 23. Transverse section showing medulla (M) and cortex (C). Scale = 10 μ m. FIGURE 24. Basal cell (BC) of monosiphonous pigmented filaments, with two filaments (HC) arising from it. Mature cortex shows rhizoidal corticating cells (Rcf). Scale = 10 μ m. FIGURE 25. Stichidium showing three cover cells (cc) over sporangium (Sp). Scale = 100 μ m. FIGURE 26. Cystocarp showing terminal position, the displaced monosiphonous filaments (H) at the base, ostiole (O), and carpospores (Cp). Scale = 1 mm.

layer. Cortical cells are about 10 μm in cross section and up to 100 μm long. The cortical layer is one to two cells thick, followed by a subcortical or medullary layer (Figure 23) composed of large, irregular cells 20–50 μm in diameter and 120–150 μm long. Subcortical cells nearest the central axial filament frequently have eight to nine conspicuous pit connections.

Monosiphonous pigmented filaments are slightly stiff and stand away from the axial surface. This is due in part to the slightly raised basal cell (Figure 24), which can be distinguished from the surrounding cortical cells by its rounded-pyramidal shape. These cells vary in size from 10 to 15 μm wide and 15 to 20 μm long. Each basal cell has two pit connections leading to two different filaments. The filaments are dichotomously branched with the Y-shaped angle, once at the base and from one to three times more; hair cells are 15–20 μm wide and 20–50 μm long, tapering toward the tips.

Tetrasporangial thalli bear stichidia up to 400 μm long that are developed from the first dichotomy of the monosiphonous filaments and are either sessile or borne on a one- to three-celled monosiphonous pedicel. Mature stichidia are lanceolate and often apiculate at the tips. Sporangia (Figure 25) are subtended by three postsporogial cover cells; the cover cells are somewhat larger than those in other species, are rounded-rectangular, and cover 1/2 of the sporogial surface.

Spermatogial plants have branches slightly more slender than branches on cystocarpic or tetrasporogial plants. The spermatogial branches are slender, flexuous, between 21 and 40 μm in diameter and up to 500 μm long.

Cystocarpic plants are common and easily distinguished in the field because they have prominent terminal cystocarps (Figures 22, 26). They are spherical, 1.0–1.5 mm in diameter and at least 1 mm high, with a rostrate ostiole 250 μm long, and near the apices of short lateral branches. Often the end of the lateral branch extends beyond the cystocarp for a short distance and the monosiphonous filaments form a mass beneath the cystocarp (Figure 26). The pericarp is similar to the cortex, being composed of small, more or less

irregular to cuboidal cells 20 by 30 μm , differing from the axial cortex in their shorter length.

HAWAIIAN COLLECTIONS: This species is common in the Hawaiian Islands, from Midway southeast through the main Hawaiian islands. Midway Islands, lagoon on east side, 1–2 m depth, leg. H. J. Fortner, 1 November 1984 (Abbott 17351, BISH); Sand Island, 10–50 m offshore of Picket Pt., leg. H. J. Fortner, 29 June 1983 (Abbott 17498, BISH). La Perouse Pinnacle, on the face of a rock wall, leg. Fred Ball, 9 July 1977 (Abbott 17282, BISH). Pearl and Hermes patch reef, leg. H. J. Fortner, 3 July 1984 (Abbott 17317, BISH). Necker Island, intertidal from a reef flat covered with sand and limestone rubble, leg. Fred Ball, 6 July 1977 (Abbott 17288). Kauai, Lawai Kai, reef flats, Schlech 227, 228, 266–268, 270–273, 281, 282 (BISH); leg. Gordon Daida, May 1979 (Abbott 14956, 15154) and March 1980 (15694, 15792, 15819, 15835, 15952); Kipukai, tide pools and reef flats, Schlech 206, 211, 263 (Schlech). Oahu, Halona-Kaloko, on basalt rocks, 21 May 1944 (Abbott 428, BISH), 4 August 1944 (Abbott 560, BISH); east of Wailupe fishpond, leg. D. P. Abbott, 1 July 1945 (Abbott 792, BISH); Kaalawai, Schlech 285 (BISH); Diamond Head, below lighthouse, leg. D. P. Abbott, 8 July 1945 (Abbott 823 and 891, BISH), Schlech 284 (BISH); Waikiki near aquarium, 12 January 1944 (Abbott 356, BISH), Schlech 214, 231 (BISH); Ala Moana, Schlech 233, 286 (BISH); West Beach, intertidal on exposed bench, leg. F. & M. Tseng, 1 March 1987 (Abbott 18056, BISH); Pupukea, intertidal, leg. Vernon Sato, 15 May 1983 (Abbott 16283, BISH); Punaluu, on reef flat, Schlech 202, 278 (BISH), 303 (holotype, BISH); Kaaawa, reef flat, Schlech 218 (BISH); Kualoa, Schlech 217 (BISH); Makapuu, intertidal benches, Schlech 230, 280 (BISH). Molokai, Halena on beach rock, leg. M. S. Doty, 27 December 1953 (MD19731, BISH). Penguin Bank, 57–58 m depth on coral rubble, 7 September 1959 (Doty 19140, BISH). Maui, Maalaea Bay, leg. T. Matsui (Doty 13524, BISH). Lanai, Naha, leg. M. S. Doty, 26 November 1960 (Doty 22042, BISH). Hawaii Island, Keahole Pt., on OTEC buoy at

45 m depth, leg. E. C. Haderlie, 22 July 1977 (Abbott 12718, BISH).

It is clear from a comparison with type material of *Eupogodon antillarum* (Howe) Silva (*Dasyopsis antillarum* Howe) that these two species are closely related. They share many features in common: overall size, branching pattern, cortex, and cross section, as well as occupying similar habitats. Differences include the characteristic iridescent color of the Hawaiian species (lost, however, on drying or preservation), the terete main axes, and the thick stipe. Howe's type specimen (Howe 5625 in New York Botanical Garden) was collected from the drift and is without its basal portions, but other specimens identified as this species do not show thick stipes. *E. antillarum* also differs in the hair basal cell, which is polysiphonous and not at all like the monosiphonous basal hair cell seen in *E. iridescens*.

Eupogodon iridescens differs from *E. pilosus* (Weber van Bosse) Silva in its spiral branching pattern and resulting three dimensionality; *E. pilosus*, being dichotomously branched, has a more planar habit. The thick stipe in *E. iridescens* is different from the small basal disc that serves as a stipe for *E. pilosus*. And, finally, *E. iridescens* has two filaments per basal cell, but *E. pilosus* has a single filament per basal cell.

Eupogodon pilosus (Weber van Bosse) Silva

Figures 27–32
Silva, 1987: 130.

BASIONYM: *Dasyopsis pilosa* Weber van Bosse, 1923: 377.

Thalli somewhat variable (Figures 27–28) in height but most are 3–5 cm tall. Main axis and branches are terete, though upper branches may be slightly spreading and variable in thickness. Some thalli have firmer, thinner axes 2 mm in diameter, others have softer, wider axes about 3 mm in diameter. Main axis is attached by a small, discoid holdfast and is erect but not stiff; color when living is dark brown, occasionally dark maroon, drying to lighter brown.

Branching is dichotomous (Figure 28), a feature distinctive at the apices, which are often antlerlike as a result of recent branching. In older thalli the dichotomous nature of the

branching may not be so obvious. Apices are densely covered with monosiphonous filaments, are slightly rounded-attenuate, and do not resemble the strongly incurved apical morphology seen in some *Dasya* species.

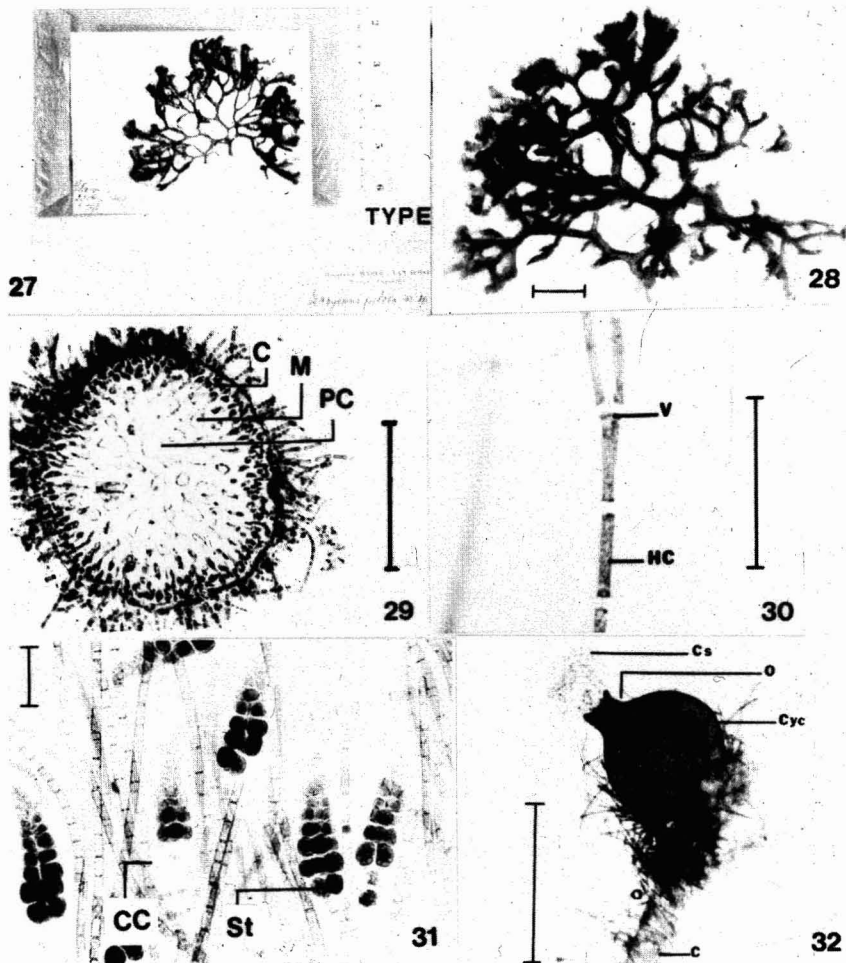
Squashes of the apex show five pericentral cells, but cross sections (Figure 29) between 5 and 10 mm of the apex reveal a central cell surrounded by seven or eight cells, which can be interpreted as being two to three being cut off by the pericentral cells as the beginning of a subcortical layer and the cortex. The number of cells, whether pericentral or subcortical, is not fixed in the immature or mature axes. Cortex is composed of thin, colored, rhizoidal cells, forming a loose network with a vertical orientation.

Branches are densely clothed with fine monosiphonous filaments; they arise randomly from the cortical cells, are not aggregated into tufts, and do not have a distinctive basal cell. Most filaments are unbranched, or branched once from the base with the narrow Y-shaped angle of branching (Figure 30). Monosiphonous pigmented filaments may reach a length of 4–5 mm; most are broken off except at the apex. Individual cells are 6–10 μm wide and 30–60 μm long.

Tetrasporangial thalli bear stichidia at the base of the monosiphonous filaments. Stichidia are sessile or borne on a one-celled pedicel and are conical when immature (Figure 31), becoming lanceolate with age. Only one stichidium is produced per filament. Mature stichidia may reach a length of 400 μm and are blunt at the apices. Two presporangial cover cells are formed per sporangium; occasionally only one cover cell can be seen, however. The cover cells are slightly rounder at the pit connection end. When the tetrasporangia fall out, the skeleton of the stichidium remains attached.

Spermatangial branches are also borne on the dichotomy at the base of the filaments. Many mature spermatangial branches have a sterile filament at the tip, three to five cells long. Length ranges vary with age, mature branches reaching 300–400 μm long, with a diameter of 20–30 μm .

Cystocarps are positioned laterally (Figure 32) on the main axes and branches, are sessile, and are about 1 mm long, including the ostiole,



FIGURES 27–32. FIGURE 27. *Eupogodon pilosus*, holotype (Leiden herbarium). FIGURE 28. Specimen from Kauai. Scale = 1 cm. FIGURE 29. Transverse section of axis showing pericentral cells (PC), medulla (M), and cortex (C). Scale = 1 mm. FIGURE 30. Monosiphonous filament cell (HC) showing Y-shaped angle of branching (V). Scale = 100 μ m. FIGURE 31. Developing stichidia (St) showing small cover cells (CC). Scale = 100 μ m. FIGURE 32. Mature cystocarp (Cyc) showing sessile, lateral position and shape, with ostiole (O) and carpospore mass (Cs). Scale = 1 mm.

which is about 100 μ m long. The pericarp is well developed and composed of cells similar to the cortex; near the ostiole the pericarp cells are arranged in chains or rows of central cells surrounded on both sides by smaller cells that later elongate to the characteristic rhizoidal shape.

HAWAIIAN COLLECTIONS: Subtidal on reef flats and possibly at deeper depths. Kauai, Kipukai, reef flat, Schlech 207–210 (BISH); Lawai Kai, *s.n.* (BISH). Oahu, Kahala Beach,

Schlech 224 (BISH); Waikiki, Schlech 242 (BISH); Sand Island reef, Schlech 292, 295 (BISH) and a floating dock at Sand Island, Schlech 302 (BISH).

Eupogodon pilosus shows a complement of characteristics that makes it unlikely to be confused with any other species in the Hawaiian Dasyaceae. The dichotomous branching pattern; the long, straight, soft monosiphonous filaments; the small discoid holdfast; and the lateral cystocarps clearly separate it from *E. iridescens*. All the features discussed

above agree well with the type specimen from New Guinea and with material from Guam. The distinctions between *Eupogodon pilosus*, *E. anastomosans*, and *Dasya adhaerens* Yamada would benefit from further examination and comparison. Observations on the scanty material of the latter two species suggest that they are synonymous and that the single entity *Eupogodon anastomosans* may be distinguished from *E. pilosus* by its irregular branching pattern.

Genus *Heterosiphonia*

Only one species of *Heterosiphonia*, *H. crispella*, is present in the Hawaiian Islands, previously listed as *H. wurdemannii* var. *laxa*. The variations shown in the sizes of the plants as well as sizes of the cells of the laterals, the branching pattern, and the formation of rhizoids suggest that the recognition of varieties is questionable. Although not easy to confuse with Hawaiian species of *Dasya* and *Eupogodon* owing to the more complex morphology of the latter genera, tetrasporangial plants of all three genera show that they must be related

because the stichidia are very similar even to the casual observer. *Heterosiphonia*, however, has two presporangial cover cells, whereas Hawaiian *Dasya* species have three postsporangial cover cells per sporangium. Two *Eupogodon* species in Hawaii have two cover cells, and *E. iridescens* has three.

Only *Heterosiphonia* among the Hawaiian *Dasyaceae* is completely uncorticated, although corticated species exist elsewhere. In Hawaii only corticated species of *Dasya* occur, and as far as is known, *Eupogodon* species are always corticated.

Heterosiphonia crispella (C. Agardh) Wynne

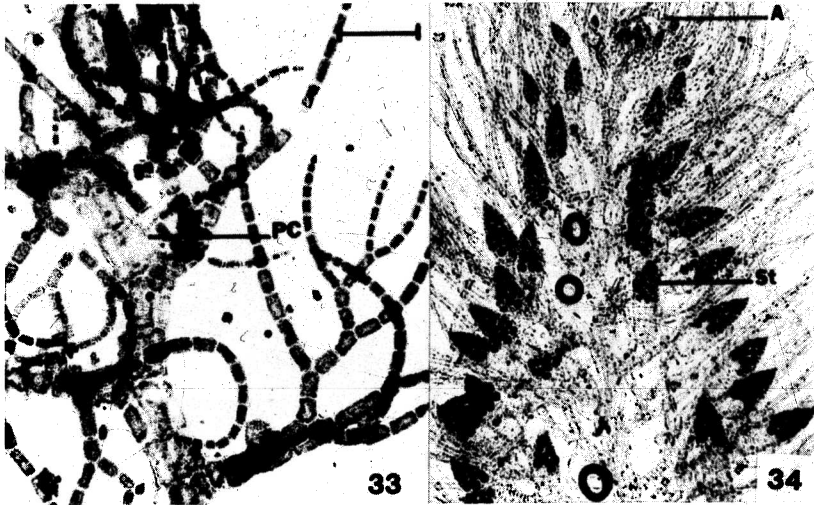
Figures 33–34

Wynne, 1985: 81–90.

BASIONYM: *Callithamnion crispellum* C. Agardh, 1828: 183.

SYNONYM: *Heterosiphonia wurdemannii* (Bailey ex Harvey) Falkenberg var. *laxa* Børgesen, 1915–1920: 327, figs. 327–328.

Thalli are small, prostrate, creeping epiphytes often found around the bases of other algae, but also on the segments of *Halimeda*



FIGURES 33–34. *Heterosiphonia crispella*. FIGURE 33. Branching pattern showing slight dorsiventrality, the long unbranched lateral that is formed with the determinate branches, and pericentral cells (PC). Scale = 1 mm. FIGURE 34. Habit of tetrasporangial thallus showing apex (A) and young stichidia (St) that are pyramidal in shape, differing from the shape of mature stichidia. Scale = 1 mm.

species and the “blades” of *Amansia glomerata*. Hawaiian specimens rarely reach more than 1 cm in length.

Main axes are composed of four pericentral cells, 80 μm long, and are uncorticated. Axes are 100 μm in diameter and alternately branched at every other segment (Figure 33). The laterals are dichotomously branched three to four times; the first dichotomy of the branches produces an unbranched lateral up to 1 mm long that is composed of cells 20 μm in diameter and 100 μm long that taper slightly toward the tip. Cells comprising the branched segments of the laterals are somewhat smaller, 20 by 50 μm . Branches are strongly incurved except for the unbranched lateral. Rhizoids develop from the main axes and commonly have disc-shaped ends; rhizoids are also formed by modification of apices of hairs, by simply elongating and becoming colorless, or by forming a digitate end.

Tetrasporangial stichidia are located at the second or third dichotomy of the branches and begin development quickly upon formation at the apex. They are at first pyramidal in shape (Figure 34) and become elongate with age, reaching lengths of 500 μm or more, and may be sessile or formed on a two- to three-celled monosiphonous pedicel. Three presporangial cover cells are formed per sporangium. The stichidia are apiculate when mature, having an otherwise somewhat cylindrical shape.

Cystocarpic plants have not been collected in Hawaii. The only spermatangial specimen known from Hawaii showed elongated spermatangial branches terminating a branch of a monosiphonous filament, or replacing one branch of a dichotomy. A filament 3–10 cells long continued beyond the spermatangia. The spermatangial branches measured up to 225 μm long and 40 μm in diameter.

HAWAIIAN COLLECTIONS: Gardner Pinnacle, at 16 m depth on a colonial ascidian, *Eudistoma* species, leg. Lisa Boucher, September, 1980, Abbott 16014, 16017 (Abbott). Necker Island, disengaged by lobster traps raised from 50–60 m depth, leg. H. J. Fortner, 8 October 1984, Abbott 17084b (Abbott); same place, disengaged by lobster traps raised from 100 m depth, leg. H. J. Fortner, 6 October 1984,

Abbott 17092 (Abbott). Kauai, Kipukai, reef flat on *Eupogodon iridescens*, Schlech 262 (BISH). Oahu, Ala Moana Park, on *Eupogodon iridescens*, Schlech 240 (BISH); dredged at 70 m depth off Honolulu Harbor on eroded coral, leg. Karen Hunt, 11 December 1980, Abbott 16004 (Abbott); Maili, subtidal at 6.5 m depth, leg. K. McDermid and E. Zablackis, 7 April 1984, Abbott 16477 (Abbott); Makaha, subtidal 7–10 m depth, leg. Lynn Hodgson, 5 August 1988, Abbott 18867 (Abbott). Maui, Kauiki Head, on dead coral at 2–3 m depth, leg. D. P. Abbott, 26 August 1976, Abbott 12647 (Abbott), 18025 (BISH); Makiwa, 1.5–2 m depth, leg. D. P. Abbott, 22 August 1978, Abbott 14393 (BISH), 14520 (Abbott). Hawaii Island, Keahole Point, on a series of core samples at 5–8 m depth, leg. Alison Kay, Fall 1981, Abbott 16027 (core no. 4); Abbott 16034 (core no. 10); Abbott 16043 (core no. 28); Abbott 16044 (core no. 19); Abbott 16065 (core no. 21), all microscope slides in Abbott collection. Abbott 16065 is the only male plant seen in Hawaii. The species is a common epiphyte, favoring subtidal situations.

Heterosiphonia crispella (as *H. wurdemannii* var. *laxa*) is one of the more frequently documented members of the Dasyaceae in the warm Pacific. The two varieties, *H. crispella* var. *crispella* (= *H. wurdemannii* var. *typica*) and *H. crispella* var. *laxa*, are both characterized by having a long unbranched arm of a lateral whose sister branch becomes dichotomously to subdichotomously divided several times. Differences were listed by Børgesen (1915–1920) in the first variety as having four to six pericentral cells, being more squarrose, with shorter branches containing larger cells and frequently digitate rhizoids (his fig. 326), whereas the variety *laxa* had more delicate, attenuate branches (his fig. 327), with four pericentral cells, and apices of many of the laterals became extended into rhizoidal ends. He suggested that perhaps differences in habitat such as shallow versus deep water might account for these differences. Hawaiian material from a variety of depths reveals plants that fit both descriptions (i.e., varieties *crispella* and *laxa*), and some of the plants showed rhizoids that had ends of laterals modified as elongated, colorless rhizoids, as well as other

branches on the same specimen ending in digitate or disc-shaped ends. A few of the plants had five pericentral cells, but most had four. We suggest that only the species should be recognized, with a range of features that would include those of the two current varieties. However, more gametangial material might aid in separating out the overlap of features that at present depend on vegetative distinctions.

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