

## Stream Macroalgae of the Hawaiian Islands: A Preliminary Study<sup>1</sup>

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**ABSTRACT:** Thirty-four stream segments sampled on the four largest Hawaiian Islands had water temperatures ranging from 20 to 27°C, neutral to alkaline pH (6.7–8.0), and relatively low ion content (30–360  $\mu\text{S cm}^{-1}$ ). Mean species number per stream segment was 3.4 and ranged from one to seven. Macroalgal cover varied considerably from <1 to >76% (mean, ca. 27%) of the stream bed. In the 114 populations of stream macroalgae collected, 34 species were found: 16 Chlorophyta, 11 Cyanophyta, five Rhodophyta, and two Chrysophyta, of which 25 are new records for Hawai'i; the morphological forms were 16 mats, eight free filaments, seven tufts, one colony, one crust, and one gelatinous filament. The most widespread species was the cyanophyte *Phormidium retzii* (C.Ag.) Gom., occurring in 18 stream segments. In terms of reproductive status of the populations sampled, 75% were vegetative, 25% were asexual, and <1% was sexual. Only one new species was collected, the rhodophyte *Batrachospermum spermatiophorum*, belonging to the Section *Contorta* and having unique colorless spermatoiphores and large whorls, carposporophytes, and carposporangia.

OCEANIC ISLANDS HAVE biotas that have never been physically part of a larger, continental community, but consist of immigrants and their descendants (Pielou 1979). They tend to have fewer species than comparable continental regions (Schoener 1988). For freshwater organisms, intolerant of high salinities, immigration most likely occurs by jump-dispersal (Pielou 1979), either by migrating birds or by wind currents (Johansson 1976). Although certain freshwater algal taxa have been collected on oceanic islands, there are few whole

floristic studies of macroscopic algae, particularly those inhabiting flowing waters. Examples of such studies include Tilden (1902) and MacCaughey (1917, 1918*a,b*) for the Hawaiian Islands, Starmach (1975) for the Seychelles, Johansson (1976) for the Azores, and Lobban et al. (1990) for Yap. However, in all of these reports, stream macroalgae represent only a fraction of the collection.

The Hawaiian Islands provide an interesting location for study because they are ca. 3700 km from the nearest continental land mass and they have been only partially examined for the freshwater biota (Maciolek 1969). Most watersheds are typically small, with steep stream channels in the headwaters, little storage capacity, and a tendency for flash flooding at times of heavy rain (Department of Geography, University of Hawaii 1983). The water tends to be low in ions and slightly turbid. Many streams have been modified by diversion for irrigation purposes. Because of the paucity of information on the stream macroalgae from these Islands, this preliminary survey was initiated.

<sup>1</sup> This research was supported by NSERC grant OGP 0105629 to R.G.S., NSERC grant 0645 to K.M.C., and NSERC grant OGP 2016 to Charles C. Davis. Manuscript accepted 2 July 1993.

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## MATERIALS AND METHODS

Thirty stream segments were sampled on the four largest islands during the period of 9–19 August 1992: nine on Kaua'i, seven on O'ahu, eight on Maui, and six on Hawai'i (Figure 1). Four additional samples were included from Kaua'i collected on 31 July and 1 August 1988 (numbers 31–34, Figure 1). At each site, a 20-m length was entirely examined for macroalgae, and cover was estimated as described previously (Sheath et al. 1986c). Maximum width and depth, mean current velocity, water temperature, pH, and specific conductance were measured, and water color was noted. Samples were immediately fixed in 2.5% calcium carbonate-buffered glutaraldehyde for identification and morphometric

analysis, Carnoy's solution for chromosome determination, and 2.5% Karnovsky's solution in cacodylate buffer for electron microscopy.

For light microscopy, samples were examined and photographed with an Olympus BHS microscope and PM-10AK photographic system. Reproductive state of each population was noted. Because an undescribed *Batrachospermum* species was collected, it was analyzed using an SMI Microcomp image analysis apparatus as described by Sheath et al. (1992). For chromosome determination, the sample was stained according to Wittmann's (1965) hematoxylin technique, and counts were made in replicates of four. Electron microscopy was done according to the methods of Sheath et al. (1977).

Cluster analysis with the unweighted group

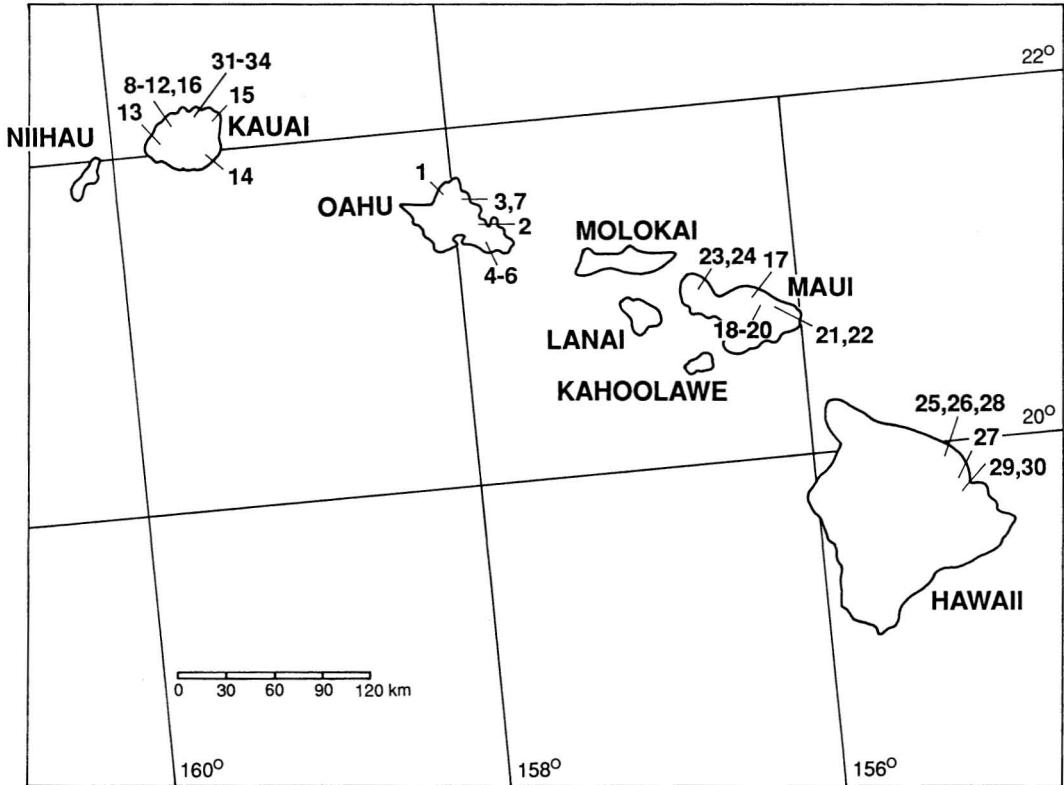


FIGURE 1. Distribution of stream segments sampled in the Hawaiian Islands. Numbers correspond to stream numbers in Table 1.

method (UPGMA) was utilized to examine possible floristic associations among Islands based on the Sørensen's Similarity Index (Mueller-Dombois and Ellenberg 1974, SAS Institute 1988). Pearson Product-Moment correlations and multiple linear regressions were determined among stream characteristics, species numbers, and cover ranks based on the Minitab statistical package (Ryan et al. 1985).

## RESULTS AND DISCUSSION

The stream segments sampled varied considerably in terms of maximum width and depth, and these two characteristics were positively correlated ( $P < 0.05$ ) (Table 1). Current velocities tended to be slow to moderate (ca. 75 cm sec<sup>-1</sup>), with the exception of stream no. 27 (96 cm sec<sup>-1</sup>), because we collected in one of the drier months (Depart-

TABLE 1  
CHARACTERISTICS OF HAWAIIAN STREAMS SAMPLED

STREAM <sup>a</sup>	MAX. WIDTH (m)	MAX. DEPTH (cm)	MEAN CURRENT VELOCITY (cm sec <sup>-1</sup> )	TEMPERATURE (°C)	pH	SPECIFIC CONDUCTANCE (μS cm <sup>-1</sup> )	WATER COLOR <sup>b</sup>	MACROALGAE	
								SPECIES NUMBERS	COVER SCALE <sup>c</sup>
1	8	50	75	25	7.5	72	0	3	4
2	5	35	33	23	7.8	160	0	2	4
3	4	50	50	22	7.0	50	0	3	3
4	3	85	50	21	7.8	85	0	5	2
5	4	85	21	21	7.4	89	0	3	1
6	4	34	25	21	7.5	110	0	3	2
7	4	35	41	22	6.7	50	0	4	5
8	1.1	11	—	20	7.8	150	0	1	4
9	8	65	69	22	8.4	91	0	5	3
10	1.5	25	13	22	7.6	120	0	4	3
11	1.4	45	10	22	7.8	120	0	3	2
12	8	>100	20	22	7.8	87	0	4	2
13	3	>100	37	20	7.0	28	1	2	2
14	6	>100	40	26	7.9	200	0	7	4
15	15	>100	29	25	8.0	100	0	4	6
16	5	>100	23	21	7.8	83	0	5	2
17	4	55	15	22	7.4	50	0	4	3
18	10	>100	18	22	7.4	40	0	3	5
19	8	55	9	24	7.3	40	0	2	2
20	4	>100	31	21	7.7	110	0	5	3
21	4	>100	36	21	7.3	30	0	4	5
22	0.9	50	4	23	7.3	38	0	5	5
23	2	30	7	27	7.8	110	0	2	2
24	8	52	44	22	7.3	54	0	4	4
25	5	50	38	21	7.7	32	0	1	3
26	0.3	4	—	21	6.9	79	0	1	4
27	4	55	96	22	7.4	50	0	3	2
28	5	>100	62	20	7.6	84	0	3	4
29	2	32	32	24	7.2	40	0	2	2
30	6	>100	0	23	7.0	—	0	2	4
31	1.5	21	—	22	—	165	0	4	3
32	10	100	—	20	—	90	—	6	3
33	0.4	9	—	23	—	360	—	3	4
34	3	18	—	23	—	240	—	2	4

<sup>a</sup>For details see Appendix.

<sup>b</sup>0; colorless; 1, yellow.

<sup>c</sup>0, 0%; 1, <1%; 2, 1–10%; 3, 11–25%; 4, 26–50%; 5, 51–75%; 6, 76–100% (Sheath et al. 1986c).

ment of Geography, University of Hawaii 1983). Water temperatures ranged from 20 to 27°C. The pH values were neutral to slightly alkaline (6.7–8.0), specific conductance was mostly low ( $\leq 240 \mu\text{S cm}^{-1}$ ), with the excep-

tion of stream no. 33 ( $360 \mu\text{S cm}^{-1}$ ), and these variables were positively correlated ( $P < 0.001$ ). All streams were colorless except for stream no. 13.

Macroalgal species numbers per stream

TABLE 2  
DISTRIBUTION OF STREAM MACROALGAE IN THE HAWAIIAN ISLANDS

TAXON	ISLAND				TOTAL NO. OF STREAMS
	KAUA'I ( $n = 9 + 4^a$ )	O'AHU ( $n = 7$ )	MAUI ( $n = 8$ )	HAWAI'I ( $n = 6$ )	
<b>Cyanophyta</b>					
<i>Phormidium inundatum</i> Kütz.*	2		2	1	5
<i>P. retzii</i> (C.Ag.) Gom.*	8	4	3	3	18
<i>P. subfuscum</i> Kütz.*	3		4		7
<i>P. tenue</i> (Menegn.) Gom.			1		1
<i>Rivularia haematites</i> (DC) C.Ag.*	1 <sup>a</sup>				1
<i>Schizothrix friesii</i> Gom.*	1		1	1	3
<i>S. lacustris</i> A.Br. ex Gom.*	2				2
<i>Scytonema arcangelii</i> Born. & Flah.*			1		1
<i>S. myochrous</i> (Dillw.) C.Ag.*		1	1		2
<i>S. tolypothricoides</i> Kütz.*			1		1
<i>Tolypothrix tenuis</i> (Kütz.) emend. Schmidt*		1			1
<b>Chlorophyta</b>					
<i>Cladophora glomerata</i> (L.) Kütz.*	4	1			5
<i>C. glomerata</i> var. <i>crassior</i> (C.Ag.) van den Hoek*			1		1
<i>C. rivularis</i> (L.) van den Hoek*		1			1
<i>Cloniophora plumosa</i> (Kütz.) emend. Bory	4	1	1		6
<i>Mougeotia</i> sp. 1			1		1
<i>Mougeotia</i> sp. 2	1				1
<i>Oedogonium</i> sp. 1		1			1
<i>Oedogonium</i> sp. 2			1		1
<i>Rhizoclonium hieroglyphicum</i> (C.Ag.) Kütz.*	1			1	2
<i>Spirogyra</i> sp. 1	6	2	4	1	13
<i>Spirogyra</i> sp. 2	1		1		2
<i>Spirogyra</i> sp. 3			1		1
<i>Stigeoclonium stagnatile</i> (Hazen) Collins*		1			1
<i>S. subsecundum</i> Kütz.*	1 <sup>a</sup>				1
<i>S. tenue</i> (C.Ag.) Kütz.	2				2
<i>Zygnema</i> sp.*		1			1
<b>Chrysophyta</b>					
<i>Hydrosera whampoensis</i> Wallich*	3	1	2		6
<i>Tribonema affine</i> (G.S.West) G.S. West*		1			1
<b>Rhodophyta</b>					
<i>Audouinella eugenea</i> (Skuja) Jao*	1 <sup>a</sup>				1
<i>A. pygmaea</i> (Kütz.) Weber-Van Bosse*	3	4		3	10
<i>Batrachospermum spermatiophorum</i> , n. sp.*			1		1
<i>Compsopogonopsis leptocladus</i> (Mont.) Krishnamurthy*	1	1	2	1	5
<i>Hildenbrandia angolensis</i> Welwitsch ex West & West*	4	2		1	7
Total	19	15	18	8	

\*New record for Hawaiian stream habitats.

<sup>a</sup>Collected by J.A.H. 31 July–1 August 1988, but not found in subsequent survey.

segment ranged from one to seven, and numbers were positively correlated to maximum depth and specific conductance ( $P < 0.05$ ). However, multiple linear regression showed that these two stream characteristics accounted for only 32% of the variability in macroalgal species numbers. The mean number of species per segment (mean, 3.4) compares closely with a mean of 3.1 species for macroalgae in streams of 10 Caribbean Islands and in 1000 streams throughout North America (Sheath and Cole 1992). Therefore, mean diversity in a localized stream segment does not appear to be affected by island size or degree of separation from a continental land mass.

The macroalgal cover varied considerably from  $< 1$  to  $> 76\%$  of the stream bottom and was positively correlated to maximum stream width ( $P < 0.05$ ) (Table 1). This correlation

may be a result of reduced shading from overhanging vegetation in wider stream segments (Sheath et al. 1986a). The mean cover in the Hawaiian streams (mean, ca. 27%) is approximately twice as high as that for North American streams, either as a whole or those in tropical regions (13–15%) (Sheath and Cole 1992). This indicates that, although Hawaiian streams vary widely in terms of macroalgal cover, more streams have larger values than those in North America.

In the 114 populations of stream macroalgae collected, 34 species were found: 16 Chlorophyta, 11 Cyanophyta, five Rhodophyta, and two Chrysophyta (Table 2). Comparing this list with previous reports of stream macroalgae from Hawai'i (Tilden 1902, MacCaughy 1917, 1918a,b, Islam 1961), 25 species are new records for stream habitats, all 11 Cyanophyta, seven Chloro-

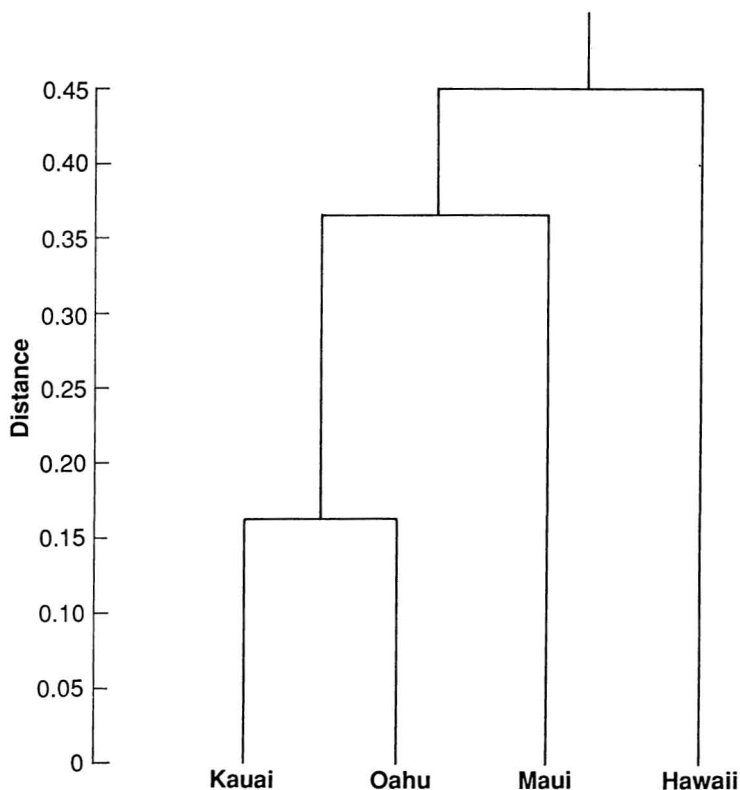
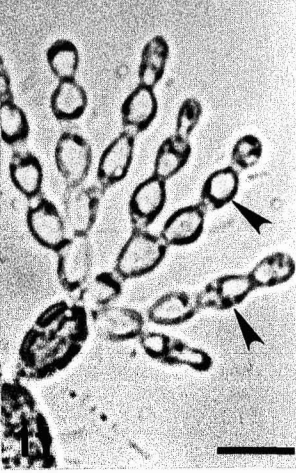
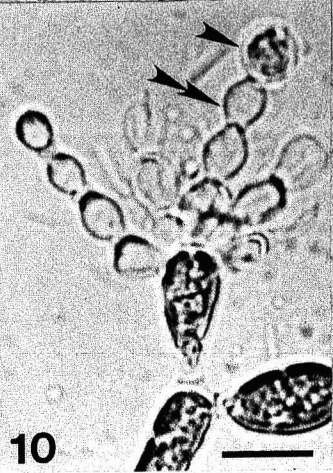
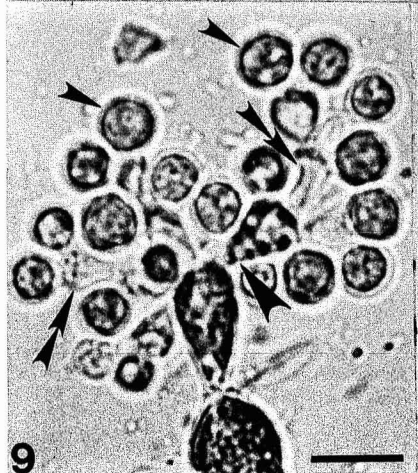
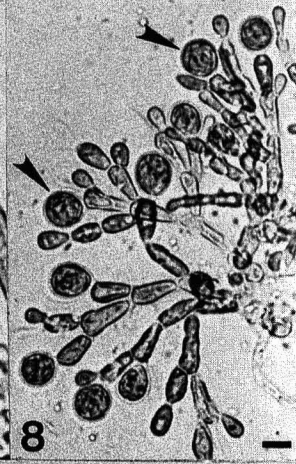
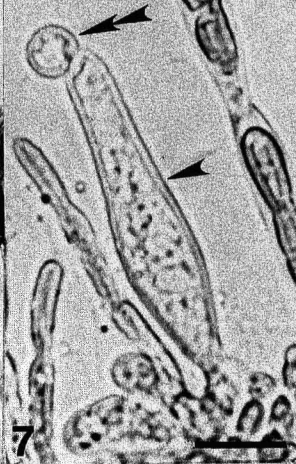
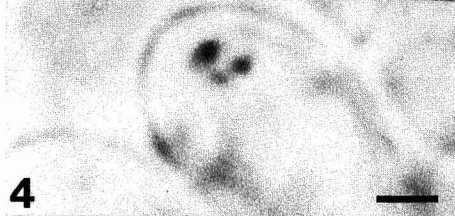
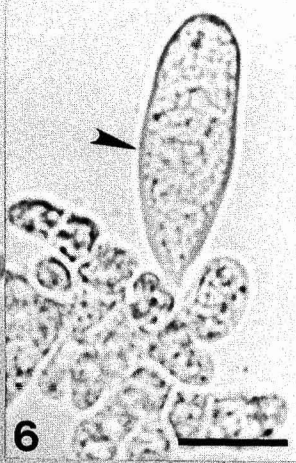
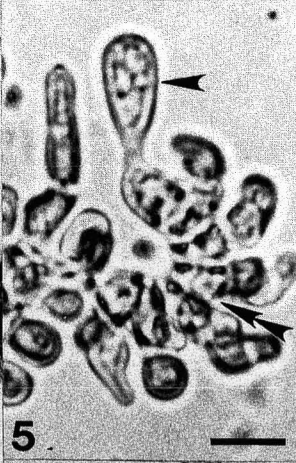
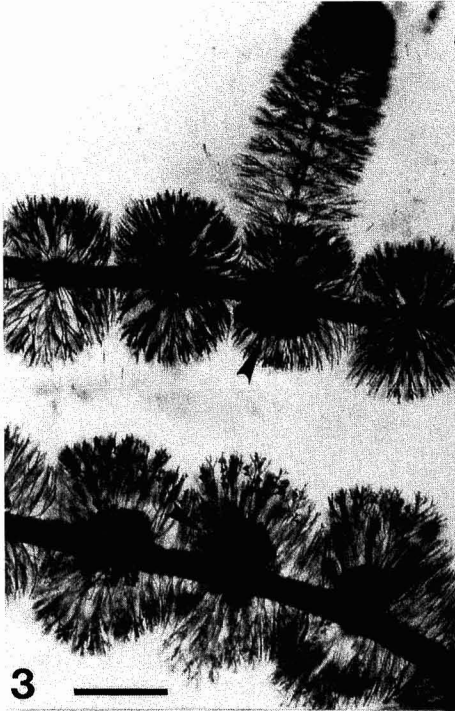


FIGURE 2. Cluster diagram showing the association of stream macroalgal species based on Sørensen's Similarity Index among the four Islands sampled.



phyta, all five Rhodophyta, and the two Chrysophyta. Of the 26 identifiable species in Hawaiian streams (Table 2), only nine were found in tropical North America, including the Caribbean Islands (Sheath and Cole 1992). Therefore, there does not appear to be a pantropical stream macroalgal flora. Only 10 of the Hawaiian species were collected from the west coast of North America (Sheath and Cole 1992), indicating that this continent is not the sole source of algal propagules for these Islands.

Fifteen to 19 species were found on Kaua'i, Maui, and O'ahu, but only eight on Hawai'i (Table 2). However, the six streams sampled on Hawai'i were localized. The cluster diagram of the species composition from each Island from the 1992 survey shows that streams on Kaua'i and O'ahu have the most similar composition, and those on Hawai'i are the most dissimilar (Figure 2). The fact that Kaua'i, O'ahu, and Maui have similar species numbers even though there is an approximate 3.5-million-year age differential (Macdonald et al. 1983) indicates that there is little relationship between age of the Island and diversity.

Of the 34 species identified from Hawaiian streams, 16 were mats, eight were free filaments, seven were tufts, and there was one each of colony, crust, and gelatinous filament (Table 2). The proportion of mats, free filaments, and crusts is similar to that of tropical streams in North America, but there is a higher percentage of tufts and lower fractions of colonies and gelatinous filaments (Sheath and Cole 1992). In terms of the reproductive status of the Hawaiian populations sampled, 75% were vegetative, 25% were asexual, and <1% were sexual. In comparison, tropical North American streams had macroalgae that

were 64% vegetative, 21% asexual, and 15% sexual (Sheath and Cole 1992).

The most widespread macroalga in Hawaiian streams was the cyanophyte *Phormidium retzii* (C.Ag.) Gom., occurring on all four Islands and in 53% of the segments sampled (Table 2). This species is the most common lotic macroalga in North America, inhabiting all biomes and 32% of tropical streams (Sheath and Cole 1992). Other frequently found Hawaiian species were the chlorophyte *Spirogyra* sp. 1 (38%) and rhodophyte *Audouinella pygmaea* (Kütz.) Weber-Van Bosse (29%) (Table 2). Eighteen of the 34 species were collected in only one stream segment.

#### DESCRIPTION OF NEW *Batrachospermum* SPECIES

*Batrachospermum spermatiophorum* Vis et Sheath, n. sp.

Figures 3–15, Table 3

LATIN DIAGNOSIS: Filum monoicum cum spermatangia super spermatiophora incololata, verticilla cupiformi, compacti, 548–1207  $\mu\text{m}$  lati, 10–14 cellulae fasciculi. Gonimoblastus semiglosus, axalis, 262–454  $\mu\text{m}$  latus, et 183–300  $\mu\text{m}$  altus, 4–8 celluluae. Fila carpogonia crispa. Carpogonia 29.3–43.1  $\mu\text{m}$  longa cum trichogyna lanceolata, 6.4–11.4  $\mu\text{m}$  lata. Carposporangia 9.3–15.4  $\mu\text{m}$  lata, 11.7–16.1  $\mu\text{m}$  longa.

DESCRIPTION: Monoecious filaments consist of barrel-shaped, compressed whorls, 548–1207  $\mu\text{m}$  wide and composed of 10–14 fascicle cells (Figure 3). Carposporophytes are axial, semiglobular, 262–454  $\mu\text{m}$  in diameter, and 183–300  $\mu\text{m}$  in height. Chromosome number in the fascicle cells is  $n = 3$  (Figure 4).

FIGURES 3–11. Light micrographs showing morphometric features of *Batrachospermum spermatiophorum*, n. sp. Scale bar = 10  $\mu\text{m}$  unless otherwise noted. (3) Two branches with barrel-shaped, compressed mature whorls containing hemispherical, axial carposporophytes (arrowheads). Scale bar = 500  $\mu\text{m}$ . (4) Hematoxylin-stained fascicle cell showing  $n = 3$  chromosomes. Scale bar = 2  $\mu\text{m}$ . (5) Immature carpogonium with inflated trichogyne (arrowhead) on curled carpogonial branch (double arrowhead). (6) Developing carpogonium with cylindrical trichogyne (arrowhead). (7) Mature carpogonium with lanceolate trichogyne (arrowhead) and attached spermatium (double arrowhead). (8) Loosely branched carposporophytes with numerous carposporangia (arrowheads). (9) Spermatangia (arrowheads) attached directly to fascicle cells (large arrowhead) or to small colorless spermatiophores (double arrowheads). (10) Spermatangium (arrowhead) at tip of three-celled, colorless spermatiophore (double arrowhead). (11) Well-developed cluster of colorless spermatiophores (arrowheads).

TABLE 3  
MORPHOMETRIC CHARACTERISTICS OF *Batrachospermum spermatiophorum*, N. SP.

WHORL DIAM.	CARPOSPOROPHYTE			FASCICLE LENGTH (CELLS)	CARPOGONIUM			CARPOSPORANGIUM		
	DIAM.	HEIGHT	CELL NO.		DIAM.	LENGTH	FORM FACTOR <sup>a</sup>	DIAM.	LENGTH	
910 (548-1207)	338 (262-454)	225 (183-300)	5.9 (4-8)	11.5 (10-14)	8.3 (6.4-11.4)	35.7 (29.3-43.1)	0.27 (0.19-0.33)	12.1 (9.3-15.4)	13.9 (11.7-16.1)	

NOTE:  $n = 30$  except carpogonia, where  $n = 15$ ; overall mean, range in parentheses. All measurements in  $\mu\text{m}$  unless otherwise indicated.  
<sup>a</sup>See Sheath et al. (1986b) for description.

The carpogonial branch is curled (Figure 5). As the carpogonium matures, the trichogyne changes from cylindrical (Figures 5-6) to lanceolate (Figure 7), with a diameter of 6.4-11.4  $\mu\text{m}$  and length of 29.3-43.1  $\mu\text{m}$ . Gonimoblast filaments are loosely branched with 4-8 cells (Figure 8). Carposporangia are spherical with a diameter of 9.3-15.4  $\mu\text{m}$  and length of 11.7-16.1  $\mu\text{m}$ .

The unique feature of this species is the existence of colorless spermatophores that are formed at the tips of fascicle filaments (Figures 9-11). Spermatangia may form directly from fascicle cells (Figure 9). However, most spermatangia (80%) occur at the apices of spermatophores, which can range from few-celled and unbranched (Figures 9-10) to multicellular and branched complexes (Figure 11).

The spermatophores were examined ultra-structurally (Figures 12-15). The pit connection between the base and subtending fascicle cell contains a typical batrachospermalean pit plug (Figure 12) having a domed outer cap layer (Pueschel 1990). The cytoplasm at all levels appears to be disrupted and in thin strands (Figures 13-14). The basal region up to the first constriction has an extra wall layer (Figure 13). Pit plugs also occur between cells of the spermatophore (Figure 14). A typical spermatangium contains numerous mitochondria and endoplasmic reticula, but no chloroplasts (Figure 15).

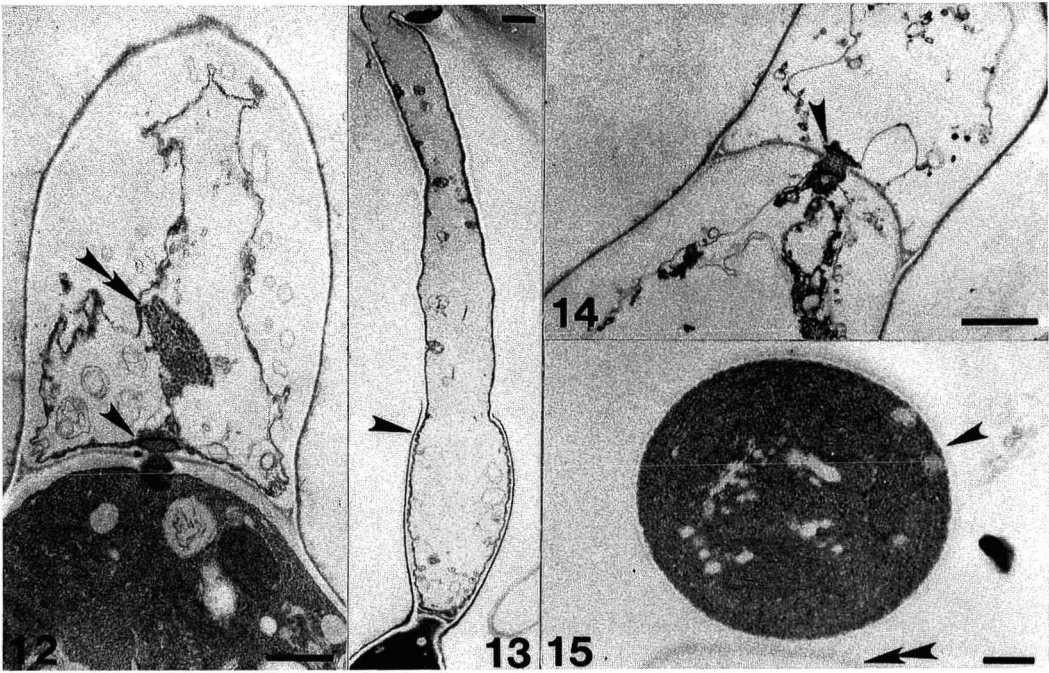
HOLOTYPE: BISH Herbarium Pacificum 628882; tributary to Waiohue Gulch at Pua'aka'a State Wayside and Route 36, Hāna District, Maui Island, collected by R. G. Sheath, 17 August 1992, stream no. 22 (Table 1).

ISOTYPE: UBC A 80848.

REMARKS: The curled carpogonial branch indicates that this species should be classified in the Section *Contorta*.

In terms of a potential origin of *Batrachospermum spermatiophorum*, within a radius of 6400 km, members of the Section *Contorta* have been reported from North America (Sheath et al. 1992), Micronesia (Kumano and Bowden-Kerby 1986), and northern Japan (Kumano and Ohsaki 1983). None of these species have spermatophores.





FIGURES 12–15. Ultrastructure of *Batrachospermum spermatiophorum*, n. sp. Scale bar = 1  $\mu\text{m}$ . (12) Spermatophore base and subtending fascicle cell showing the adjoining pit plug (arrowhead) and disrupted appearance of cytoplasm (double arrowhead). (13) Spermatophore with basal outer wall layer (arrowhead) and slight constrictions along the length. (14) Cross wall between two spermatophore cells with connecting pit plug (arrowhead). (15) Spermatangium (arrowhead) closely associated with spermatophore wall (double arrowhead).

TABLE 4

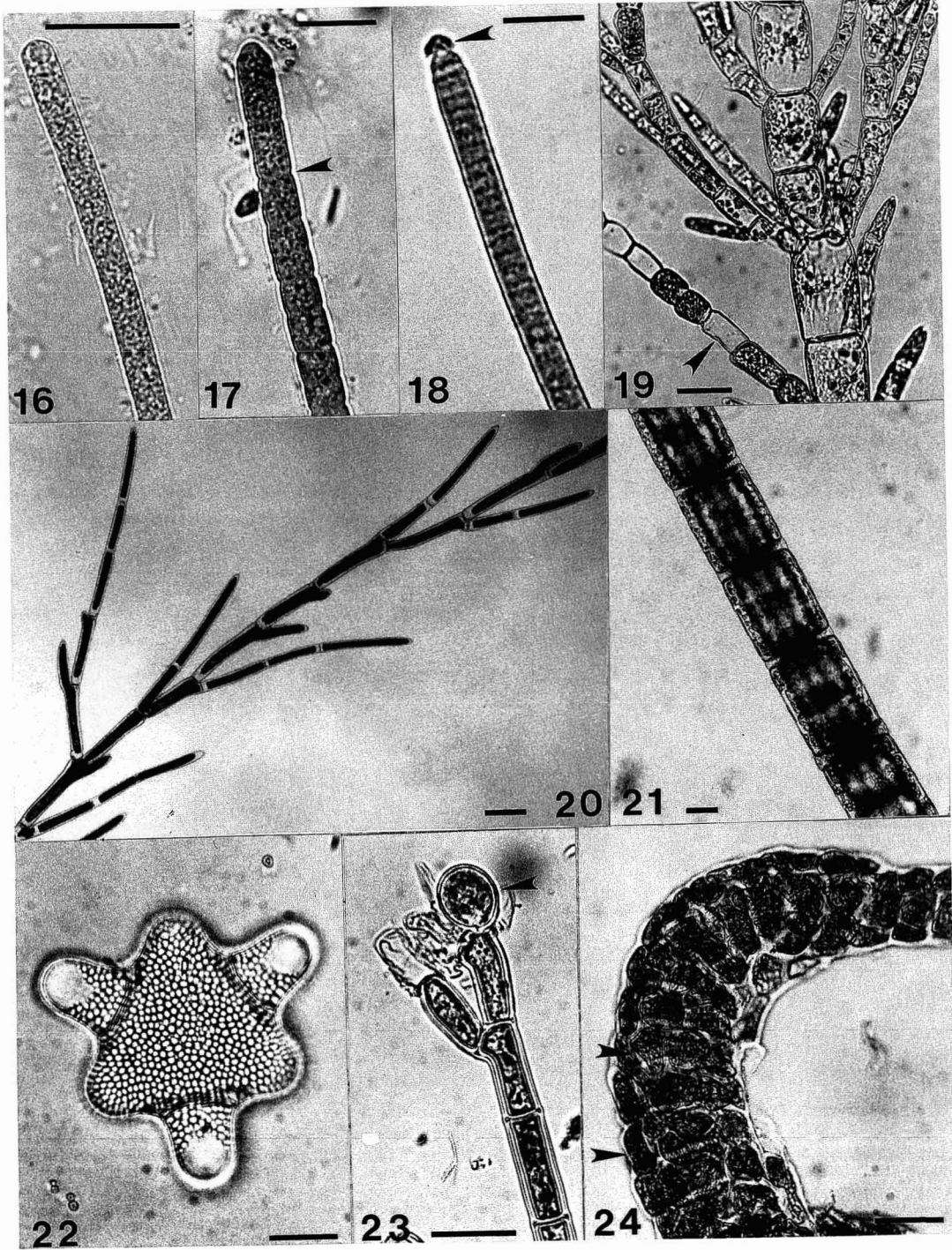
COMPARISON OF RANGES IN MORPHOMETRIC CHARACTERISTICS FOR HAWAIIAN, NORTH AMERICAN (SHEATH ET AL. 1992), MICRONESIAN (KUMANO AND BOWDEN-KERBY 1986), AND NORTHERN JAPANESE (KUMANO AND OHSAKI 1983) *Batrachospermum* SPECIES OF THE SECTION *Contorta*

LOCATION	WHORL DIAM.	CARPOSPOROPHYTE		
		DIAM.	HEIGHT	CARPOSPORANGIUM DIAM.
Hawai'i	548–1,207	262–454	183–300	9.3–15.4
North America	171–595	89–394	56–305	5.1–13.9
Micronesia	250–550	140–300	80–250	7–14
Northern Japan	300–350	80–190	40–130	7–9

NOTE: All measurements in  $\mu\text{m}$ .

In addition, diameters of the whorls, carposporophytes and carposporangia, and height of the carposporophyte are all smaller than those of the Hawaiian plants (Table 4). Therefore, *B. spermatiophorum* appears to be a distinct species.

Another species of *Batrachospermum* has been collected at 'Akaka Falls, Hawai'i Island (I. A. Abbott, pers. comm.). However, this population cannot be identified to species because of a lack of carposporangia. It can be classified in the Section *Aristatae* because



of its well-differentiated carpogonial branch. Other unpublished herbarium specimens of *Batrachospermum* from the Hawaiian Islands are as follows: (1) UC 752177, in mountains, Kaua'i, 13–14 August 1909, Minnie Read; unidentifiable because of distortion. (2) MO in UC 25833 and NY 2714, bog at head of the Wahiawa River, Kaua'i, 12 August 1895, A. A. Heller; cf. *B. kushiroense* Kumano & Ohsaki, 1983: 158; Section *Contorta* but quite distinct from *B. spermatiophorum* (Table 4).

#### CONCLUSIONS

This study has shown that with only a relatively small number of streams examined, 25 species were added to the Hawaiian flora and one new species was described. Clearly, further research is needed to fully understand the distributional patterns and biogeography of stream macroalgae inhabiting oceanic islands.

To aid in the identification of the common stream macroalgae of the Hawaiian Islands, we have included figures with brief descriptions of most species (Figures 16–24).

#### ACKNOWLEDGMENTS

Assistance in collection from Lynn Hodgson and Mary Koske and in preparation of the manuscript from Christine Everson and Roy and Sylvia Ficken is gratefully acknowledged. We thank the phycologists of the University of Hawaii for their kind hospitality and Isabella Abbott for loaning the specimen

from 'Akaka Falls from her personal collection. Specimens from NY and UC are also appreciated.

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FIGURES 16–24. Common stream macroalgae of the Hawaiian Islands. Scale bar = 20  $\mu\text{m}$  unless otherwise noted. (16) *Phormidium inundatum* bluish, unbranched filament with thin sheath and quadrate cells not constricted at cross walls (stream no. 29). (17) *Phormidium retzii* bluish, unbranched filament with barely discernible sheath and elongate cells with slight constriction at cross walls (arrowhead) (no. 2). (18) *Phormidium subfuscum* bluish, unbranched filament with barely discernible sheath, short cells with no constriction at cross walls, and prominent apical cap (arrowhead) (no. 13). (19) *Cloniophora plumosa* greenish, verticillate branched filament with cylindrical main axial cells that are much larger than those of the branches. Note zoosporangia on branch (arrowhead) (no. 3). (20) *Cladophora glomerata* var. *crassior* greenish, alternately branched filament. This variety differs from the nominate variety in having more intercalary growth (no. 20). Scale bar = 200  $\mu\text{m}$ . (21–22) *Hydrosera whampoensis* golden-colored chains as seen in girdle view (21) and with a triangular, undulate valve view (22) (no. 6). (23) *Audouinella pygmaea* bluish, sparsely branched filament with apical monosporangium (arrowhead) (no. 2). (24) *Compsopogonopsis leptocladus* bluish filament consisting of a uniseriate main axis covered by small cortical cells, some of which are rhizoidal (arrowheads) (no. 4). Scale bar = 100  $\mu\text{m}$ .

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## APPENDIX

## LOCATION OF HAWAIIAN SAMPLING SITES

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1. Waimea Falls outflow, off Route 83, Waialua District, O'ahu
  2. Waiāhole and Route 83, Ko'olau Poko District, O'ahu
  3. Kaluanui Stream at Sacred Falls State Park ca. 0.8 km west of Route 83, Ko'olau Loa District, O'ahu
  4. Mānoa Falls (Waihi Stream), Honolulu District, O'ahu
  5. Waihi Stream, ca. 0.8 km south of Mānoa Falls, Honolulu District, O'ahu
  6. 'Aihualama Stream, ca. 1.2 km south of Mānoa Falls, Honolulu District, O'ahu
  7. Kaluanui Stream at Sacred Falls State Park, ca. 1.2 km west of Route 83, Ko'olau Loa District, O'ahu
  8. Ca. 1.5 km west of Makana on Kalalau Trail, Hanalei District, Kaua'i
  9. Hanakāpī'ai Stream mouth, ca. 2 km west of Makana on Kalalau Trail, Hanalei District, Kaua'i
  10. Ca. 2.5 km southwest of Makana, Hanalei District, Kaua'i
  11. Ca. 3 km southwest of Makana, Hanalei District, Kaua'i

## LOCATION OF HAWAIIAN SAMPLING SITES (continued)

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12. Hanakāpī'ai Stream just north of falls ca. 2.5 km southwest of Makana, Hanalei District, Kaua'i
  13. Kōke'e Road 1.4 km south of Waimea Canyon Lookout split with Route 550, Waimea District, Kaua'i
  14. Route 50, ca. 5 km west of Puhi, Kamo'oloa Stream at Pu'uana Road, Līhu'e District, Kaua'i
  15. Anahola, Ka'alua Stream at Route 56 and Kiko'o Loop, Kawaihau District, Kaua'i
  16. Limahuli Stream at Makana at entrance to Hā'ena State Park, Hanalei District, Kaua'i
  17. Honopou Stream south of diversion at Route 36 at 9-mile marker, Makawao District, Maui
  18. Puohokamoa Stream at Route 36 at 11-mile marker, Hāna District, Maui
  19. 0.2 km west of 14-mile marker on Route 36, Hāna District, Maui
  20. Halfway point on Route 36 (Uncle Harry's), Hāna District, Maui
  21. Waiohue Gulch at Pua'aka'a Wayside and Route 36, Hāna District, Maui
  22. Tributary to Waiohue Gulch at Pua'aka'a Wayside and Route 36, Hāna District, Maui
  23. Waiōla'i Stream ("Earthquake water") at Route 340, Wailuku District, Maui
  24. Makamaka'ole River at Route 340, Wailuku District, Maui
  25. Small falls on walkway to 'Akaka Falls viewpoint at end of Route 220, South Hilo District, Hawai'i
  26. Small trickle on trail to 'Akaka Falls viewpoint at end of Route 220, South Hilo District, Hawai'i
  27. Kawainui Stream at Scenic Drive, 3.2 km from Route 19, South Hilo District, Hawai'i
  28. Main stream at 'Akaka Falls State Park, South Hilo District, Hawai'i
  29. Tributary of Wailuku River at Rainbow Falls viewpoint off Waiānuenu Avenue, South Hilo District, Hawai'i
  30. 'Alenaio Stream off Route 19, Hilo, South Hilo District, Hawai'i
  - 31–32. Tributary and trunk of Wainiha River, 2.5 km south of Wainiha, Hanalei District, Kaua'i
  - 33–34. Spring and stream at Kauapea Beach, Hanalei District, Kaua'i
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