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AN IMPORTANT SYSTEMATIC CHARACTER

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ABSTRACT

Newly elucidated features which can be used for taxonomic purposes are shown by the pre-fertilization procarp structure in species of the red alga *Bostrychia* Mont. Because female gametophytes are apparently rare in Caribbean field populations, having been seldom collected, these reproductive characteristics have not been evaluated previously, but may provide greater stability to the systematics of *Bostrychia* which is now based almost entirely on vegetative characteristics.

Four species of *Bostrychia*, as known from the Caribbean, *B. montagnei* Harv., *B. binderi* Harv., *B. tenella* (Lamour.) J. Ag., and *B. radicans* f. *moniliformis* Post, and one taxon of uncertain status, *B. sp.?*, were grown in culture and showed species specific features. Pre-fertilization structures that were quantified revealed differences in the length and width of trichogynes, the distribution and number of procarps present in fertile regions of the branchlets, and the number of cells of the fertile region. These differences show that reproductive structures are important taxonomic characters for species of *Bostrychia* and support the suggestion that *Bostrychia* is a primitive genus in the Rhodomelaceae.

INTRODUCTION

The red algal genus *Bostrychia* Montagne (1842, p.39) (Ceramiales, Rhodomelaceae) is widespread, occurring from tropical to cool-temperate regions, and usually associated with mangroves. The pre-fertilization arrangements of cells and development of the carpogonial branch for the nearly twenty known species of *Bostrychia* are for the most part unknown or undescribed. In the tropical and subtropical western Atlantic there are eight species recorded (Wynne 1986), and gametangial plants have been apparently rarely collected or reported.

Four tropical western Atlantic species, *B. montagnei* Harv., *B. binderi* Harv., *B. tenella* (Lamour.) J. Ag., and *B. radicans* f. *moniliformis* Post, represent members in 3 of the 8 groups presented in the artificial key of Post (1936). Based on characters of the vegetative morphology, one of these subgeneric groups includes the warm-water *B. montagnei* which is most closely related to, but does not overlap in distribution, with *B. arbuscula* Hook. et Harv. (an endemic to New Zealand), and a widely distributed, cool-water species, *B. scorpioides* (Huds.) Mont. ex Kütz. (Sluiman 1978; Prud'homme van Reine & Sluiman 1980). Another subgeneric group, *B. binderi*, *B. tenella*, and *B. calliptera* (Mont.) Mont. overlap in warm-water Pacific and Atlantic regions. Additionally, *B. binderi* and *B. tenella* have many morphological similarities, but have been separated on the nature of siphonous branchlets (e.g., Post 1936; Tseng 1943; Taylor 1960; Oliveira Filho 1977; Cordeiro-Marino 1978; Schnetter & Bula Meyer 1982; but see also Børgesen 1937; Tokida 1939; Puttock & King 1987; King et al. 1988). A third

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group, all ecorticate species, includes the world-wide *B. radicans* (Mont.) Mont., a new species from Japan, *B. pinnata* J. Tanaka et Chihara, and a south Pacific species, *B. kelanensis* Grun. ex Post, which have had gametangial phases illustrated (Möbius 1889; Cordeiro-Marino 1978; Tanaka & Chihara 1984a-b; King & Puttock 1986).

Because little emphasis has been placed on reproductive morphologies for species of *Bostrychia*, no previous comparisons have been made among species on the basis of procarpic morphologies. Here, we describe the construction and positioning of procarps in four species and one taxon of uncertain status, and based on vegetative morphology, compare their construction with morphologically related taxa. We also examine how differences in stages of procarpic development are taxonomically significant.

MATERIALS AND METHODS

Culture techniques

Isolates for culture were collected, from February 1986 to March 1987, growing primarily on the prop roots of red mangrove (*Rhizophora mangle* L.) or occasionally on rocky substrate from five sites in Florida: *B. montagnei* from the Marquesas Keys (Lat. 24° 36' N, Long. 82° 07' W); *B. binderi* from Clarence Higgs Memorial Beach Park, Key West (Lat. 24° 32' N, Long. 81° 47' W); *B. tenella* from the north side of Key West (Lat. 24° 34' N, Long. 81° 46' W); *B.* sp.?, a taxon of uncertain status, from the southeast side of Big Pine Key (Lat. 24° 38' N, Long. 81° 19' W); and *B. radicans* f. *moniliformis* from Little Jim Inlet, Indian River (vicinity of Ft. Pierce), east coast of central Florida (Lat. 27° 40' N, Long. 80° 26' W). An additional collection of fertile *B. montagnei* was made from the red mangroves at Twin Cays on the Belizean barrier reef, off central Belize (Lat. 16° 48' N, Long. 88° 05' W).

Whole female plants with prominent cystocarps were cleaned of contaminants and placed in 100 mls of 0.22 μm Millepore-filtered seawater, enriched to a concentration of 1% Provasoli Enriched Seawater (PES) (McLachlan 1973) under culture numbers of C. M. Smith, *#CMS* -10087 to -12038. Thalli were grown under a 14:10 light-dark regime at < 100 μmol quanta from fluorescent cool-white light bulbs at a temperature of 25 $^{\circ}$C and salinity of 32 $^{\circ}$/oo.

Media were changed approximately every two months. At the end of the first interval, nutrient levels were increased to 10 % PES; all other conditions were held constant.

After trichogynes were first observed, specimens were liquid preserved in 5% buffered Formalin/seawater, acidified in 2% HCl/distilled water, stained with aniline blue, and permanently mounted in serial dilutions of KARO clear syrup with phenol added as a preservative on microscope slides (Tsuda & Abbott 1985).

All our specimens from Florida and Belize were identified following Taylor (1960: 594-600), based on the taxonomic concepts of Post (1936). Voucher specimens, including microscope slides are deposited in the Algal Collection of the U.S. National Herbarium, National Museum of Natural History, Smithsonian Institution (US).

RESULTS

Procarps of Bostrychia montagnei

Fertile branches for *B. montagnei* from the Marquesas Keys, Florida were first observed from cultured plants eight months after collection, in culture *#CMS* -10104. Fertile branches of whole,

dioecious thalli were somewhat inflated, markedly curved at the apex, and polysiphonous throughout (Fig. 1). Carpogonial branches for each axial cell began about 6 cells ± 1.68 (mean ± 1 S.D., n=13 branches) behind a branch apex, and extended to a mean of 13.3 cells ± 6.51 (mean ± 1 S.D., n=13 branches) and were also observed to the 25th axial cell.

Procarps were four-celled, carpogonial branches consisting of a carpogonium with an elongate trichogyne, borne above three cells which were connected via the supporting cell to the central axis (Fig. 2). The three carpogonial branch cells were separated from the supporting cell, and visually distinct from sterile cells. Carpogonial branch cells were discoid to ellipsoid in shape and non-granular in appearance, while the supporting cell was ±rectangular and granular. Usually one procarp per axial cell was present, although the location of the procarp appeared to be restricted in development to one of two fertile pericentral cells, both on the distal side of a fertile branch of mean length 19.1 cells ± 8.05 (mean ± 1 S.D., n=13 branches) (Fig. 1). A mean of 5.8 procarps ± 3.79 (mean ± 1 S.D., n=13 procarps) was observed over an average extent of fertile region composed of 8.3 cells ± 6.02 (mean ± 1 S.D., n=13 branches).

The mean length of mature trichogynes was 142.5 μm ± 22.01 (mean ± 1 S.D., n= 10 trichogynes). These long trichogynes had a marked sheath surrounding the protoplasmic strand, with a mean width of 8.5 μm ± 0.76 (mean ± 1 S.D., n=10 trichogynes). A basal collar of cell wall through which the trichogyne passed out of the cell wall of the fertile branchlet and a distinctive "cap" at the distal end of the tube sheath were marked features of these trichogynes (Figs. 2, 3).

Another notable feature of female *B. montagnei* in culture was the occurrence of sterile branches with monosiphonous tips. These thalli always had polysiphonous branches, but, in all long branches, there were monosiphonous portions which ranged up to 36 cells with a mean of 20.9 cells ± 6.88 (mean ± 1 S.D., n=12 branches) for branches which had a mean total length of 40.3 cells ± 8.18 (mean ± 1 S.D., n=12 branches). This monosiphonous branch tip in *B. montagnei* was also illustrated by Joly (1954, pl. III:fig. 3, as "*B. scorpioides* var. *montagnei*") in Brazilian material.

Similar results were found in procarps among individuals of *B. montagnei* cultured from the Twin Cays, Belize populations.

Procarps of B. binderi

Procarps of *B. binderi* were easily observed in fertile branches within the first month of culturing whole, fertile female thalli, collected from Clarence Higgs Memorial Beach Park, Key West, Florida, #*CMS*-12025.

Mature and immature procarps were found from cell four to cell eight behind the apex, with a mean distance of 5.6 cells ± 1.52 (mean ± 1 S.D., n=5 branches) for the first fertile cell behind the apical cell. These branches ranged in length from 11 to over 16 cells, with a mean of 13.6 cells ± 1.82 (mean ± 1 S.D., n=5 branches). In fertile branches, there was one procarp per fertile axial cell, and only one axial cell bore a procarp for each branch (n=6) (Fig. 4).

Mean length of mature trichogynes was 87.1 μm ± 14.36 (mean ± 1 S.D., n=4 trichogynes) with a width of 2.9 μm ± 1.50 (mean ± 1 S.D., n=4 trichogynes), and a slight bulbous tip (Fig. 5), but no pronounced collar at the base. From the apical 3 mm of this fertile thallus, all branchlets had polysiphonous bases, and had a mean of 12.7 monosiphonous cells ± 4.04 or 76.0 % of a total branch had monosiphonous cells (mean ± 1 S.D., n=18 branches) over a mean branch length of 17.1 ± 4.98 cells (mean ± 1 S. D., n=18 branches).

Procarps of B. tenella

Procarps of *B. tenella* were observed within the first year of collection, in cultured whole thalli from mangrove roots on the northeast side of Key West, Florida. This material, *CMS #*-10087 was not reproductive at the time of collection from the field site, but within 12 months produced procarps.

Procarps occurred from cell 4 to cell 11 behind the apical cells, with a mean of from cell 4.9 ± 0.92 (mean ± 1 S.D., n = 14) to cell 10.8 ± 2.05 (mean ±1 S.D., n = 14) (Fig. 15). A mean of four procarps were observed over that fertile cell range in branches which were on the average 15.8 cells long ± 3.29 (mean ± 1 S.D., n = 14 branches) (Fig. 6).

This isolate had mature trichogynes with a mean length of 64.0 μm ± 17.27 (mean ± 1 S.D., n = 10 trichogynes), and mean width of 8.1 μm ± 0.74 (mean ± 1 S.D., n = 10 trichogynes). Trichogynes had lightly stained basal collars and inflated tips (Fig. 7).

Branches were nearly completely monosiphonous, with 11.7 cells ± 1.57 monosiphonous cells (mean ± 1 S.D., n = 18 branches) , or 97.9 % ± 4.40 of the cells in branches which were 11.9 cells long ± 1.70 (mean ± 1 S.D., n = 18 branches).

Procarps of B. sp.?, *a taxon of uncertain status*

Fertile branches of *B*. sp. ?, which has some vegetative features of both *B. binderi* and *B. tenella*, were observed in cultured whole, fertile female thalli, one month after collection. This field-collected specimen, *CMS#*-12037, was from the red mangroves in a salt flat on the Atlantic Ocean side of Big Pine Key, Florida Keys. Fertile branchlets were polysiphonous from the base to apex; the apical cells were small and difficult to distinguish.

Procarps were dense, compact arrangements of small cells located on inflated branchlets (Fig. 8), and were observed to start at the 2nd to the 23rd cell in a branch, with a mean from cell 3.2 ± 0.98 (mean ± 1 S.D., n = 14) to cell 17.8 ± 5.00 (mean ± 1 S.D., n = 14) (Fig. 15), in branches which had a mean length of 24.4 cells ± 6.03 (mean ± 1 S.D., n = 14 branches). As many as 23 procarps were counted for 8 fertile axial cells indicating that multiple procarps were supported by a single axial cell, with a mean of 12.3 procarps ± 5.45 (mean ± 1 S.D., n = 14 procarps) over fertile range of 14.3 axial cells ± 4.62 (mean ± 1 S.D., n = 14 branches).

Mature trichogynes had a mean length of 183.0 μm ± 28.12 (mean ± 1 S.D., n = 12 trichogynes), and mean width was 6.6 μm ± 0.94 (mean ± 1 S.D., n = 12 trichogynes). There was no apparent collar at the base, but the tip of the trichogyne was slightly inflated (Figs. 9, 10).

Figures 1 to 3 (to right). Procarp features of *Bostrychia montagnei*. Fig. 1. An inflated, curved, fertile branchlet. Scale = 50 μm. Fig. 2. A carpogonial branch showing the basal collar at the cell wall. Scale = 5 μm. Fig. 3. Detail of the cap at the distal end of a trichogyne. Scale = 5 μm. (A C = axial cell; C 1, C 2, and C 3 = cells of the carpogonial branch; Carp = carpogonium; Supp c = supporting cell).

Figures 4 to 5 (to right). Procarp features of *Bostrychia binderi*. Fig. 4. A non-inflated, straight fertile branchlet. Scale = 50 μm. Fig. 5. Detail of slightly bulbous tip of a trichogyne. Scale = 5 μm. (For abbreviations, see legend for Figs. 1 to 3.)
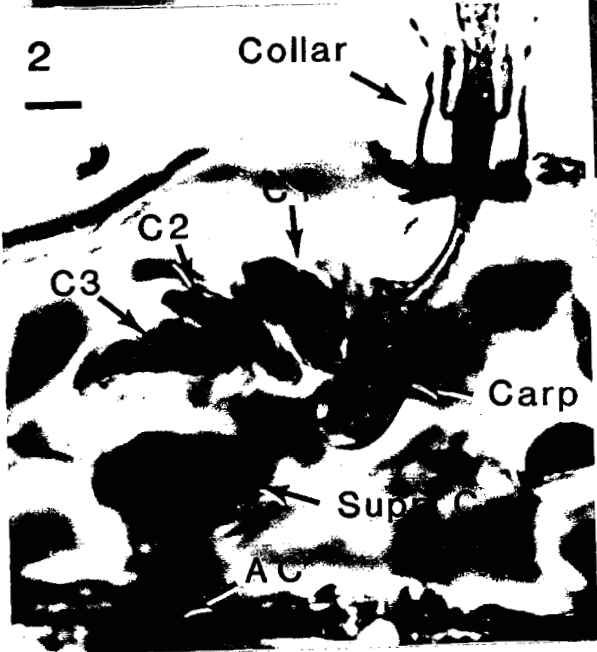
Figures 6 to 7 (to right). Procarp features of *Bostrychia tenella*. Fig. 6. An inflated, curved, fertile branchlet. Scale = 50 μm. Fig. 7. A carpogonial branch showing the basal collar at the cell wall, and the inflated tip at the distal end of a trichogyne. Scale = 5 μm. (For abbreviations, see legend for Figs. 1 to 3.)
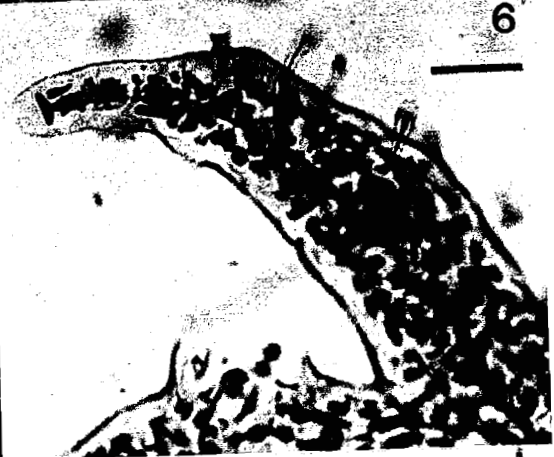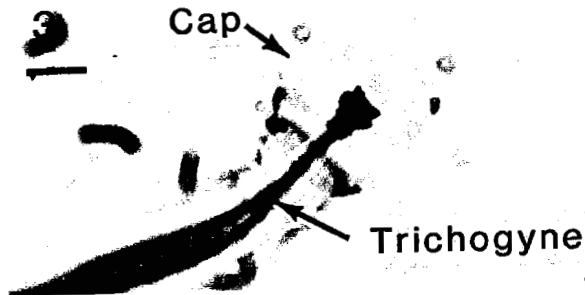
1

2 Collar

C2
C3

Carp

Sup C

A C

3 Cap

Trichogyne

6

7 Cap

Collar

C1
C2
Carp
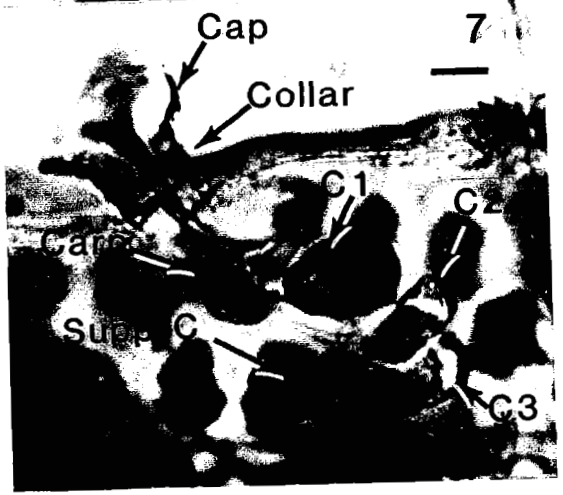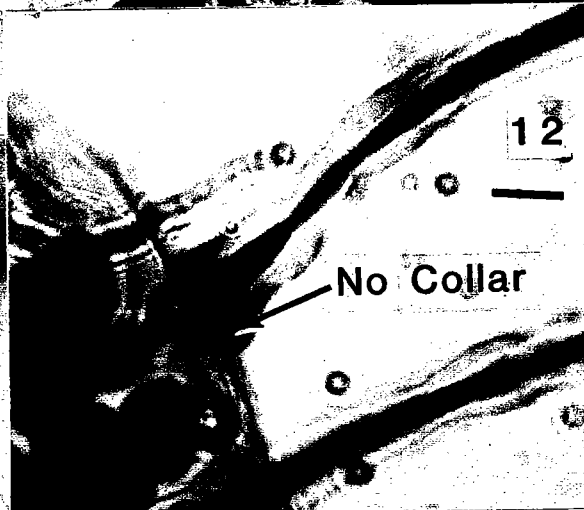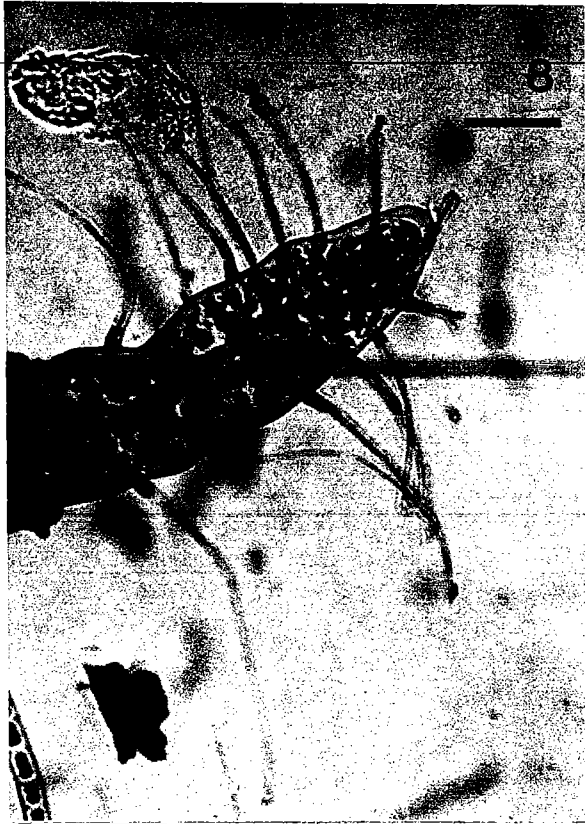
Sup C

C3

8

11

No Collar

No Collar

12

13

Trichogyne

Completely monosiphonous branchlets were not observed, although branches had monosiphonous portions of 34.7 cells long ± 10.34 (mean ± 1 S.D., n=18 branches), or 86.2 % ± 8.63 of branches which had mean length 43.0 cells ± 16.83 (mean ± 1 S.D., n=18).

Procarps of B. radicans *f.* moniliformis

Procarps of *B. radicans* f. *moniliformis* were easily observed in cultured whole, fertile female thalli, within the first month of collection, from Little Jim Islet, in the Indian River, vicinity of Fort Pierce, east (=Atlantic) coast of central Florida.

Procarps were found as early as the 2nd cell behind the apex, with a mean occurrence of 3.3 cells ± 0.75 (mean ± 1 S.D., n=12 branches) behind the apical cell (Fig. 15). Fertile regions extended to a mean of cell 5.8 ± 1.20 (mean ± 1 S.D., n=12 branches) on branches 9.25 cells long ± 2.8 (mean ± 1 S.D., n=12 branches). A mean of 2.7 procarps ± 0.78 (mean ± 1 S.D., n=12 procarps) was observed over fertile regions of 3.6 ±1.16 cells in length (mean ± 1 S.D., n=12 branches) (Fig. 11).

The mean length of mature trichogynes was 134.3 μm ± 17.60 (mean ± 1 S.D., n=12 trichogynes), with a mean width of 5.0 μm ± 0.99 (mean ± 1 S.D., n=12 trichogynes). Of the trichogynes studied, 11 of 12 lacked an aparent basal collar (Fig. 12). However, a stained collar at the base of a trichogyne was observed once. The tips of the trichogynes were not inflated nor did they have caps (Figs. 12, 13).

DISCUSSION

The goal of this research was to describe procarp structure and placement for four taxa, plus one taxon of uncertain status of *Bostrychia*, which on the grounds of vegetative morphology belong to three of the groups of Post (1936). As expected, construction of carpogonial branches of *B. montagnei, B. binderi, B. tenella, B. radicans* f. *moniliformis, B.* sp.?, and other more distantly related *Bostrychia* species are similar based on numbers of cells in a carpogonial branch (Table 1). The number of cells in a carpogonial branch , where known, was almost always four. However, Kumano (1988) reported mostly 3 celled carpogonial branches, and noted that a 4 celled carpogonial branch was observed only once in Japanese *B. flagellifera*.

Variability does exist among these species however, at the levels of organization for carpogonial branches. Differences among these taxa are seen in such features as: (1) size (lengths and widths) of the trichogynes (Fig. 14); (2) constructional details of trichogynes (e.g., presence or absence of distal caps and/or basal collars); (3) the numbers of procarps borne on an axial cell; and (4) the extent (i.e., numbers of cells) of fertile areas in a branchlet (Fig. 15).

The greatest trichogyne length, mean = 183 μm, was found for *B.* sp.?, the taxon of uncertain status. Size of this isolate's trichogyne did overlap with *B. montagnei* but was statistically distinct from

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Figures 8 to 10 (to left). Procarp features of *B.* sp. ?. Fig. 8. An inflated, curved, fertile branchlet. Scale = 50 μm. Fig. 9. A carpogonial branch showing the lack of a basal collar at the cell wall. Scale = 5 μm. Fig. 10. Detail of the slightly inflated tip at the distal end of a trichogyne. Scale = 5 μm. (For abbreviations, see legend for Figs. 1 to 3.)

Figures 11 to 13 (to left). Procarp features of *Bostrychia radicans* f. *moniliformis*. Fig. 11. An inflated, curved, fertile branchlet. Scale = 50 μm. Fig. 12. A carpogonial branch showing the lack of a basal collar at the cell wall. Scale = 5 μm. Fig. 13. Detail of the regular, non-inflated distal end of a trichogyne. Scale = 5 μm. (For abbreviations, see legend for Figs. 1 to 3.)

Table 1. Comparison of features for species of _Bostrychia_ where procarps have been described.

Species	# cells/ cpbr	# cp/ax cell	fertile cell range	branch type	mean trichogyne length
B. arbuscula[3]	4	1 to 4	3 to 9th	NA	30*
B. binderi	4	only 1/ br	4 to 8th (but only 1 cell)	str	87.1
B. sp.?	4	1 to 2	2 to 23th	cur	183.0
B. kelanensis[5]	4	1 to 2	4 to 10th	str	80*
B. montagnei	4	1 to 2	6 to 25th	cur	142.6
B. pinnata[4]	4	1	4 to 10th	cur	60.5
B. radicans[1] f. moniliformis Brazil	4	1?	NA	NA	72.7
B. radicans f. moniliformis Florida	4	1	2 to 7th	cur	134.3
B. scorpioides[2]	4	1?	NA	NA	54*
B. tenella	4	1	4 to 11th	cur	64.0
B. flagellifera[6]	3(-4)	1	3 to 4th	NA	200.0

Key to terms: br= branch; cpbr= carpogonial branch; cur = curved; NA = not available; str = straight; * = mature trichogyne length may not have been illustrated.

References: [1] Cordeiro-Marino 1978; [2] Falkenberg 1901; [3] Hommersand 1963; [4] King & Puttock 1986; [5] Tanaka & Chihara 1984b; [6]Kumano 1988.

all other *Bostrychia* species by this length criterion. Trichogynes were shortest for *B. binderi* (mean = 87 μm) and *B. tenella* (mean = 64 μm); the differences were not statistically significant between these two species. These two, however, did differ statistically in the width of trichogynes. While the lenghts were clearly different, the trichogyne widths for *B. tenella* and *B. sp.?* did overlap (Fig. 14).

The presence or absence of trichogyne features, such as an inflated cap at the distal end of a trichogyne or a basal collar at the location where a trichogyne left the cell wall of a fertile region, varied among the species studied. *Bostrychia montagnei* had the most pronounced collars, which stained densely to reveal some constructional details, and had the most obvious inflated tips. *Bostrychia binderi* and *B. tenella* had inflated tips but neither had obvious or lightly stained collars. Trichogyne tips for *B.* sp.? appeared less inflated than other species while the basal collars were more prominent. *Bostrychia radicans* f. *moniliformis* showed neither of these features.

The numbers of procarps borne per axial cell also differed among these species. *Bostrychia* sp.? bore a mean of more than 12 mature procarps or withered trichogynes on a mean of 14 axial cells in a fertile range, while *B. binderi* was found to have only one procarp on an entire branch. *Bostrychia tenella*, in mean figures, had four procarps over about a six cell fertile region.

Differences in the extents of axial cells or parts of a branch which become fertile, occurred among these species of *Bostrychia* (Fig. 15). For *B.* sp. ? and *B. montagnei*, the range over which procarps and fertilized carpogonial branches extended past the 20th axial cell in fertile branches was (means) 14.3 and 8.3 cells, respectively. In contrast, for *B. radicans* f. *moniliformis* and *B. binderi*, they did not extend past the seventh cell, yielding substantially smaller fertile regions on branches (means = 3.6 and 6.5 cells, respectively). This difference may be attributable to generally shorter branches of these species.
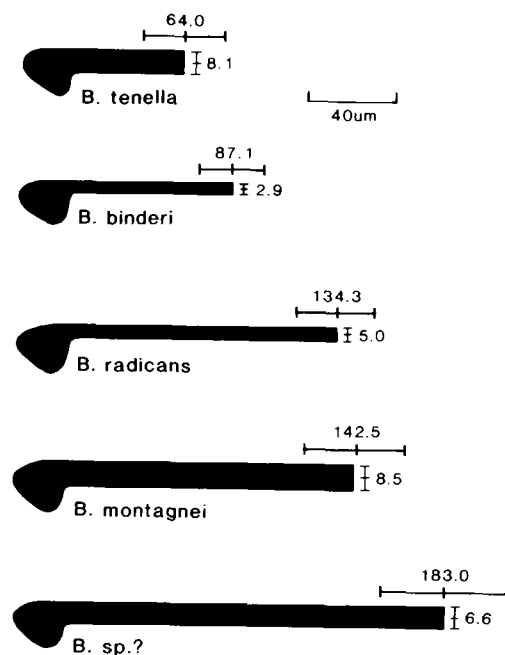

Figure 14. Diagrammatic comparison of trichogyne lengths and widths (X ± 1 S.D.) for five species of *Bostrychia* studied.

The extent of stability of these procarp features is unknown. For example, J. A. West (pers. comm.) found some variation in his culture isolates of other *Bostrychia* entities. Trichogyne length was longer for his isolates of *B. binderi* and *B. tenella* than those reported here, and there was some variation in numbers of procarps on a fertile branch. While it must be ascertained that these variations are not artifacts of culture conditions, comparisons between different populations in culture may reveal important biogeographic or temporal variations among populations of *Bostrychia*, or raise taxonomic questions. In another red alga, *Batrachospermum* Bory, trichogyne length was significant as a feature of the species, with the length of trichogynes correlated with branchlet length of the species (R. G. Sheath, pers. comm.).

The fate of multiple fertile procarps in a branch where fertile regions extend over multiple cells or, the fate of multiple procarps on the same axial cell appear to differ with the development of spermatangia or tetrasporangia. All our study material, and illustrations in published accounts, suggest that only one mature cystocarp develops per branch (e.g., Harvey 1853, Plate 14C, Fig. 2; Børgesen 1918, Fig. 303; Newton 1931, Fig. 206G; Joly 1965, Fig. 640; Cordeiro-Marino 1978, Fig. 351; Tanaka & Chihara 1984b, Fig.4-2; Prud'homme van Reine & Sluiman 1980, Fig. 11). Thus, in contrast to branches in which 10 or more axial cells bear spermatangia (Smith & Norris 1988) or tetrasporangia (Smith & Norris unpubl. data), the production of carposporangia appears to be developmentally regulated and restricted to one site for each branch, even though 20 or more procarps may be present on that branch.

Developmental restrictions may be necessary to eliminate all but one cystocarp because of the relatively large size of a mature cystocarp, and the way a cystocarp is devoloped on a branch, exteriorly rather than modifications produced when developed on branches, as generally occurs for spermatangia or being embedded in the stichidial branchlets as are the tetrasporangia in this genus. Possibly, the energetic costs of a developing cystocarp may stress nearby gametophytic cells so as to eliminate other cystocarps. Hommersand (1963, p. 255) suggests that limitations actually develop at the time of fertilization "... in a group of procarps the development of the first one to be fertilized causes the development of all the others to be suppressed at the stage at which the auxiliary cell is normally cut off."

Because a large fertile region has procarps at all developmental stages, it is likely that numerous procarps increase the probability of fertilization by extending the time when mature females are present. The large trichogynes most likely have increased the area of receptive surfaces available to bind spermatia. Although we lack data to test this hypothesis, this reasoning suggests that selection could favor red algal species which bear numerous, large-celled trichogynes on multiple branches of each thallus.

Procarps of B. montagnei *and close relatives*

Based upon construction of procarps of *B. arbuscula*, *B. scorpioides* and *B. montagnei*, the three species vary considerably: *B. arbuscula* and *B. scorpioides* have shorter trichogynes, 30 and 54 μm respectively, (Table 1) compared to the longer trichogynes of *B. montagnei*, (142.6 μm; Table 1, Fig. 14); *B. arbuscula* has 1 to 4 procarps per axial cell, while *B. montagnei* has 1 to 2; the fertile axial cells of *B. arbuscula* were from the 4th to the 6th axial cells, while in *B. montagnei* they extended from the 7th to 25th cells. In contrast for Caribbean *B. montagnei* there was little variation between Marquesas Keys (Florida) and Belize (Central America) populations studied. There was also little difference between the structure and occurrence of spermatangia in the isolates of *B. montagnei* from the Florida Keys and Belize (Smith & Norris 1988).

Procarps of B. binderi *and* B. tenella

The validity of separating *B. binderi* and *B. tenella* as distinct taxa has been controversial primarily because of the monosiphonous versus polysiphonous nature of branchlets which would seem to be a highly variable vegetative feature. For example, Post (1936) and Tseng (1943) considered them separate taxa, while Børgesen (1937), Tokida (1939), Puttock and King (1987), and King et al. (1988) considered them as one species.
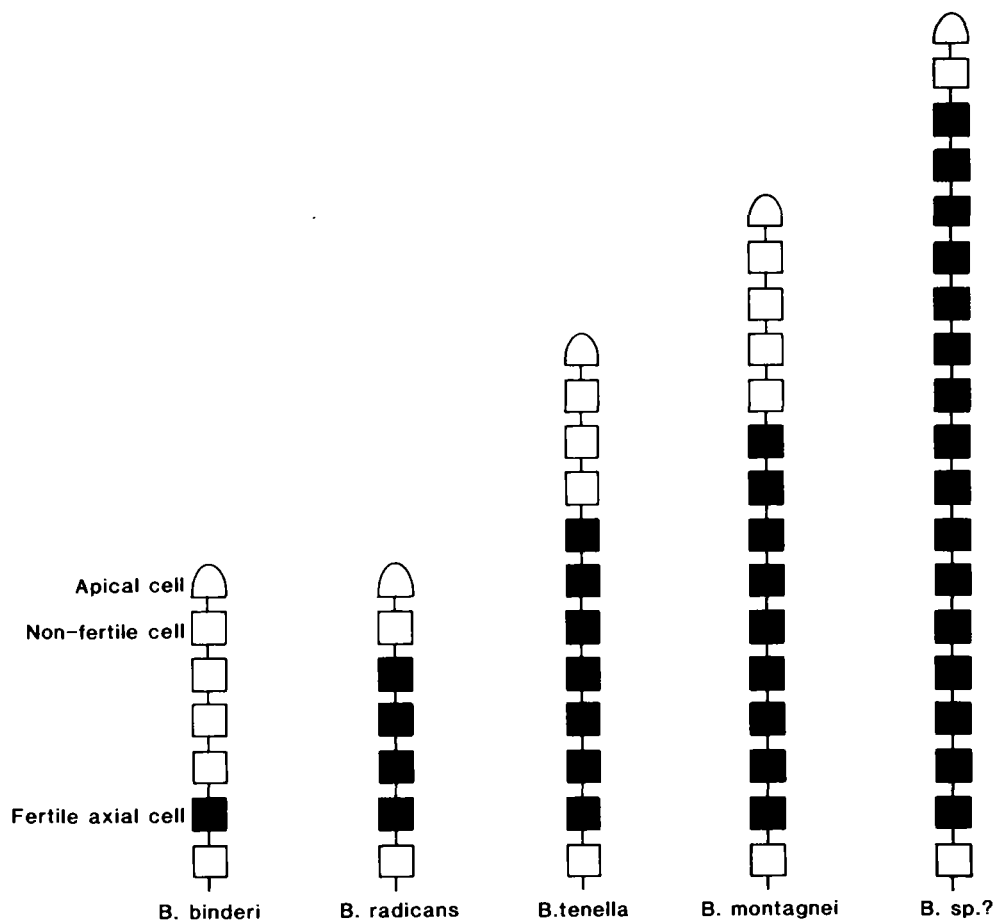

Figure 15. Diagrammatic comparison of the extent of axial cells in the fertile region of branchlets, which were seen to bear carpogonia distally from the branchlet apical cell (X of first and last cells seen fertile; based on multiple observations) in the five species studied.

The Caribbean isolates identified as *B. binderi* and *B. tenella* differed significantly in female reproductive structures when comparing the trichogynes, the number of procarps borne in the fertile axial cells of a single branch (only one in *B. binderi* vs. mean of 4 in *B. tenella*), and in the numbers of fertile axial cells per branch (Table 1; Figs. 14-15).

Differences in patterns of spermatangial production for these species also suggests that isolates of *B. binderi* from Puerto Rico (Caribbean Sea) and *B. tenella* from Tonga (southwest Pacific Ocean) are closely allied but not identical (Smith & Norris 1988). Comparative studies of the type specimen and type-locality material *B. tenella* from St. Croix, Virgin Islands (Post 1936) must be accomplished to confirm if spermatangial observations by Falkenberg (1901) of male *B. tenella* from Tonga are the same. Additionally, comparative reproductive and vegetative studies of the Puerto Rican, Tongan and specimens identified as *B. tenella* from other localities must be made with the type and type-locality specimens.

Reproductive comparisons with the other taxon in this group, *B. calliptera*, are limited by the lack of any description of its female or male reproductive structures.

Procarps of B. sp.?, *the taxon of uncertain status*

Based upon features of vegetative morphology, *B.* sp.?, with its polysiphonous/monosiphonous branchlets shows branchlet characteristics ascribed to *B. binderi* and *B. tenella*. Yet, while it has some vegetative morphological similarities, it also has distinct features of procarpic structure which statistically separate this entity from both Caribbean *B. binderi* and *B. tenella* (Table 1; Figs. 14-15). It is possible that the Florida Keys specimens represent: (1) a hybrid between *B. binderi* and *B. tenella*; (2) a polyploid of one of the species; or (3) a new species. Comparative studies of tetrasporangial and spermatangial specimens of *B.* sp.? with those of *B. binderi* and *B. tenella* are needed before its taxonomic status can be resolved.

Procarps of B. radicans *and close relatives*

Procarps of *B. radicans* f. *moniliformis* Post from southern Brazil (Cordeiro-Marino 1978) and *B. radicans* f. *moniliformis* from central Florida have similarly elongated trichogynes (Table 1; Fig. 14). What is not known for the Brazilian specimens is the extent of variation in placement of carpogonial branches and number per axial cell among populations, while for the Florida specimens there was 1 procarp per axial cell from the 2nd to 7th cell axial cells [for the Floridian isolate see Table 1; Figs. 14-15]. *Bostrychia kelanensis* has one to two procarps per axial cell from the fourth to the tenth axial cells (Tanaka & Chihara 1984b), while the other ecorticate species, *B. pinnata* as known in Australia, is illustrated with three or four cells in a carpogonial branch (King & Puttock 1986). Female structures are unknown in the another ecorticate member of this group, *B. moritziana* (Sond. ex Kütz.) J. Ag.

CONCLUSIONS

The four species and one taxon of uncertain status of *Bostrychia* as known in the Caribbean exhibited distinctiveness in their procarpic structures, number and placement of procarps per axial cell, trichogyne size, and the occurrence of basal collars and/or distal caps on the trichogyne. Even though these characters are not readily evident to the naked eye on direct examination of field collections, our data suggest that these previously unused procarpic reproductive features are important in the systematics of *Bostrychia*. Based on use of these procarpic features, *B.* sp.? is distinct from both *B. binderi* and *B. tenella*, even though all three share some vegetative branch similarities. We suggest that *B.* sp. ? from the Florida Keys represents either a hybrid, a polyploid or a new species. Studies of the morphometrics of these entities and on their spermatangial and tetrasporangial thalli are needed to clarify their relationships.

Differences in placement and construction of female reproductive systems has been observed for another primitive red algal assemblage, the Nemaliales (see e.g., Abbott 1976). It is possible that the differences observed here in construction and placement of carpogonial branches among these Caribbean species may be attributable to the primitive state of *Bostrychia* within the family.

Since there is only one careful post-fertilization study of *Bostrychia* (i.e., *B. arbuscula* by Hommersand, 1963), comparisons of pre- and post-fertilization events for other species of *Bostrychia* should be investigated to test the validity of the procarp characters we proposed herein to be used in the systematics of the genus. Future studies should include investigating the range of both interspecific and intraspecific variation among field populations and culture conditions to test the stability of these characters over a range of conditions. And finally, while we observed differences in procarp structure among the Caribbean species we studied that correlate with the artificial groups suggested by Post (1936) in her key to the species, we recognize that these subgeneric groupings must be critically tested as well.

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