

Structure and Occurrence of Spermatangia in Caribbean *Bostrychia montagnei* HARVEY and *B. binderi* HARVEY (Rhodomelaceae, Ceramiales)

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Plants of *Bostrychia montagnei* HARV. and *B. binderi* HARV. in culture conditions show different patterns of spermatangial development, and are described here for the first time. Male thalli of *B. montagnei* produced spermatangia continuously over a fertile branch, from the third to at least the 44th axial cell. Four primary parent cells were found per axial cell of recurved, fertile branches. Each primary parent cell (PPC) was pit-connected to at least three spermatium producing, secondary parent cells (SPC). A PPC bore as many as 19 cells in a dense aggregate, 4 of which were SPCs, and 15 immature and mature spermatia.

Male thalli of *B. binderi* produced spermatangia from the second to at least the 23rd axial cell. Four to five PPCs were observed borne from each axial cell of fertile areas on straight branches. Each PPC was pit-connected to a single secondary parent cell, which in turn was pit-connected to two SPCs and formed a row of cells. A PPC bore as many as 24 cells, 8 of which were SPCs, and 16 spermatia. For *B. binderi*, spermatangia produced by an individual branch could occur in as many as four distinct areas.

Spermatangial structures also differed among the closely related species group of *B. montagnei*, *B. arbuscula* HOOK. et HARV., *B. scorpioides* (HUDS.) MONT. ex KÜTZ. Similarly, spermatangial formation differed between closely related species, *B. binderi* and *B. tenella* (LAMOUR.) J. AG. These differences among male reproductive structures suggest that they may be important in the systematics of *Bostrychia* MONT. The simple nature of spermatangial construction among species of *Bostrychia* suggests that this is a primitive genus in the Rhodomelaceae.

Key Index Words: Bostrychia—mangrove algae—Rhodophyta—Rhodomelaceae—species concepts—spermatangia

The taxonomy of the red algal genus *Bostrychia* MONTAGNE (1842) (Rhodomelaceae, Ceramiales) is based exclusively on vegetative morphology, and includes several subgeneric groups (POST 1936). For example, within the group "Flagellifulcratae" (POST 1936:7) is a subgroup of *B. scorpioides* (HUDS.) MONT. ex KÜTZ., *B. arbuscula* HOOK. et HARV. and *B. montagnei* HARV. that has 1) haptera derived from pericentral cells, 2) two pericentral cells per axis cell when viewed laterally, 3) at least one layer of cortication, 4) no differentiation between upright and prostrate axes, and 5) only polysiphonous ultimate branchlets.

These species differ in the extent of cortication, and form of main axes (POST 1936).

Another subgroup of "Flagellifulcratae" (POST 1936:6) is composed of *B. binderi* HARV. and *B. tenella* (LAMOUR.) J. AG., which share haptera derived from pericentral cells, and have one to three layers of cortication, but *B. calliptera* MONT. differs from the latter two in having a cortex of rhizoidal filaments (POST 1936). The siphonous nature of branchlets differs among these species (POST 1936; TSENG 1943).

These taxonomic characters given by POST (1936) have been widely accepted and used to identify species of *Bostrychia* (e.g.,

TSENG 1943; DAWSON 1954; JOLY 1954; TAYLOR 1960; WOMERSLEY and BAILEY 1970; TSUDA and WRAY 1977; CORDEIRO-MARINO 1978; KUMANO 1979; LAWSON and JOHN 1982; SCHNETTER and BULA-MEYER 1982; TANAKA and CHIHARA 1984 a, b; KING and PUTTOCK 1986; LEWIS and NORRIS 1987; SILVA *et al.* 1987). Use of vegetative morphology for species definitions, possibly because of the apparent rarity of reproductive thalli in field collections, has resulted in few detailed descriptions for gametangial and tetrasporangial stages of *Bostrychia* species. About one third of the known species have spermatangial plants described in detail (FALKENBERG 1901; NEWTON 1931; HOMMERSAND 1963; PRUD'HOMME VAN REINE and SLUIMAN 1980; TANAKA and CHIHARA 1984; KING and PUTTOCK 1986).

Reproductive structures used as taxonomic characters, as are so widely employed in the taxonomy of other algae, have been rarely employed in the systematics of *Bostrychia*. Here, we describe spermatangial development in *B. montagnei* HARV. (1853) and *B. binderi* HARV. (1848), species which represent different subgroups in the genus. Our work indicates that male thalli are not only useful to the taxonomy of *Bostrychia*, but represent phylogenetic markers for the family Rhodomelaceae.

Materials and Methods

Isolates for culture of *B. montagnei* were collected in February and March 1986 from red mangrove prop roots (*Rhizophora mangle* L.) growing at Twin Cays, Belize (Lat. 16°48' N, Long. 88°05' W) and Big Pine Key, Florida, U.S.A. (Lat. 24°39' N, Long. 81°20' W). Whole plants were cleaned of contaminants and placed in 100 mls of 0.22 μm Millepore-filtered seawater, enriched to 1% of Enriched Seawater Recipe (PES) (MCLACHLAN 1973) at 32‰ salinity, under culture numbers CMS -10011, -10040, -10079 and -10086. Cultured isolates of *B. binderi* from Puerto Rico were obtained from John A. WEST, University of

California, under culture number JAW 2514. Thalli of both species were allowed to grow under a 14:10 L:D at <100 μmol quanta from fluorescent cool white bulbs, at a temperature of 25°C.

Media was changed approximately every two months. At the end of the first interval, nutrient levels were elevated by a 10% increase in PES; all other conditions were held constant.

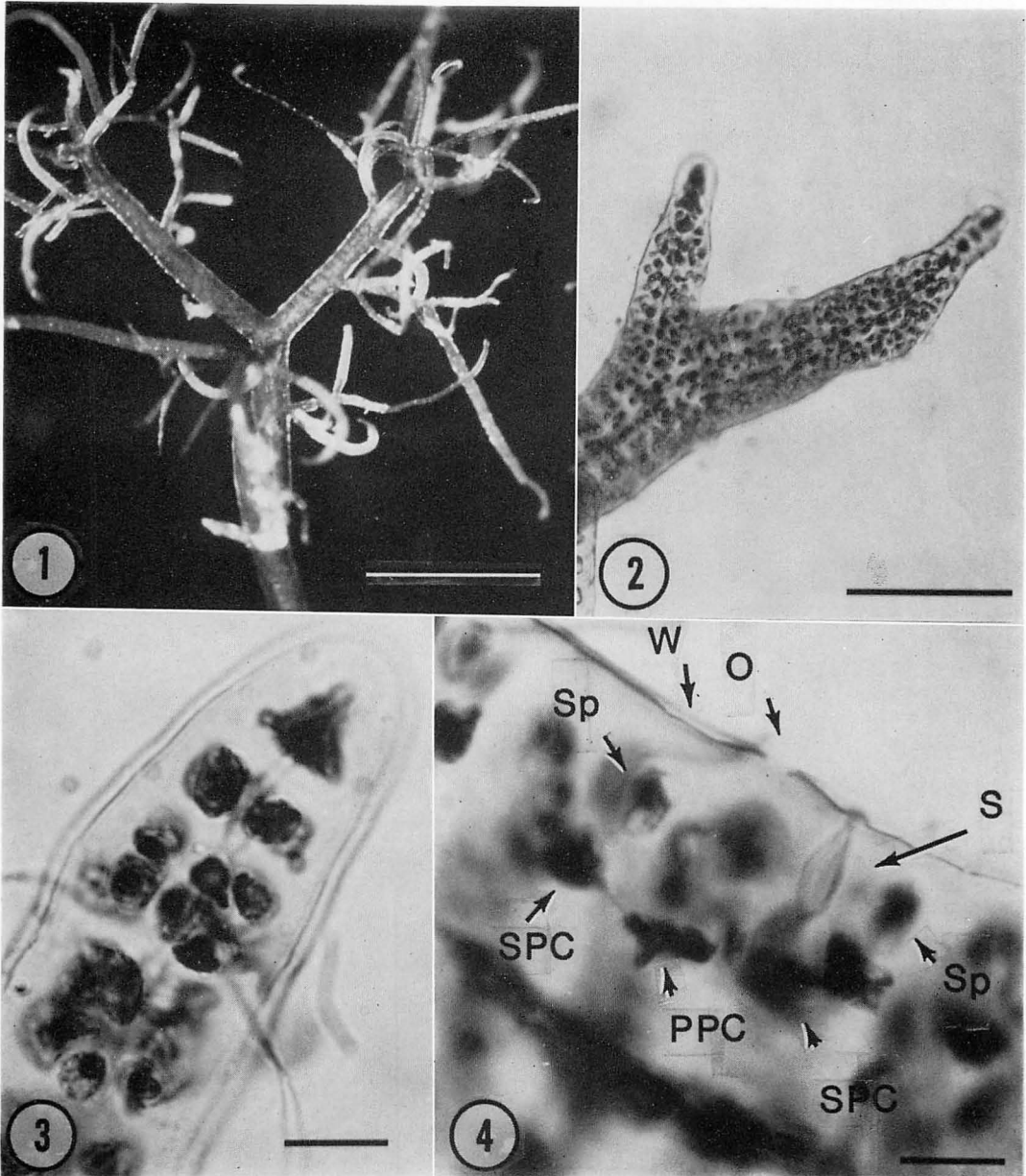
Specimens for morphological study were stained with aniline blue, and permanently mounted on microscope slides (TSUDA and ABBOTT 1985). Voucher specimens and microscope slides are deposited in the Algal Collection of the U.S. National Herbarium (US), National Museum of Natural History, Smithsonian Institution, Washington D.C., U.S.A.

Results

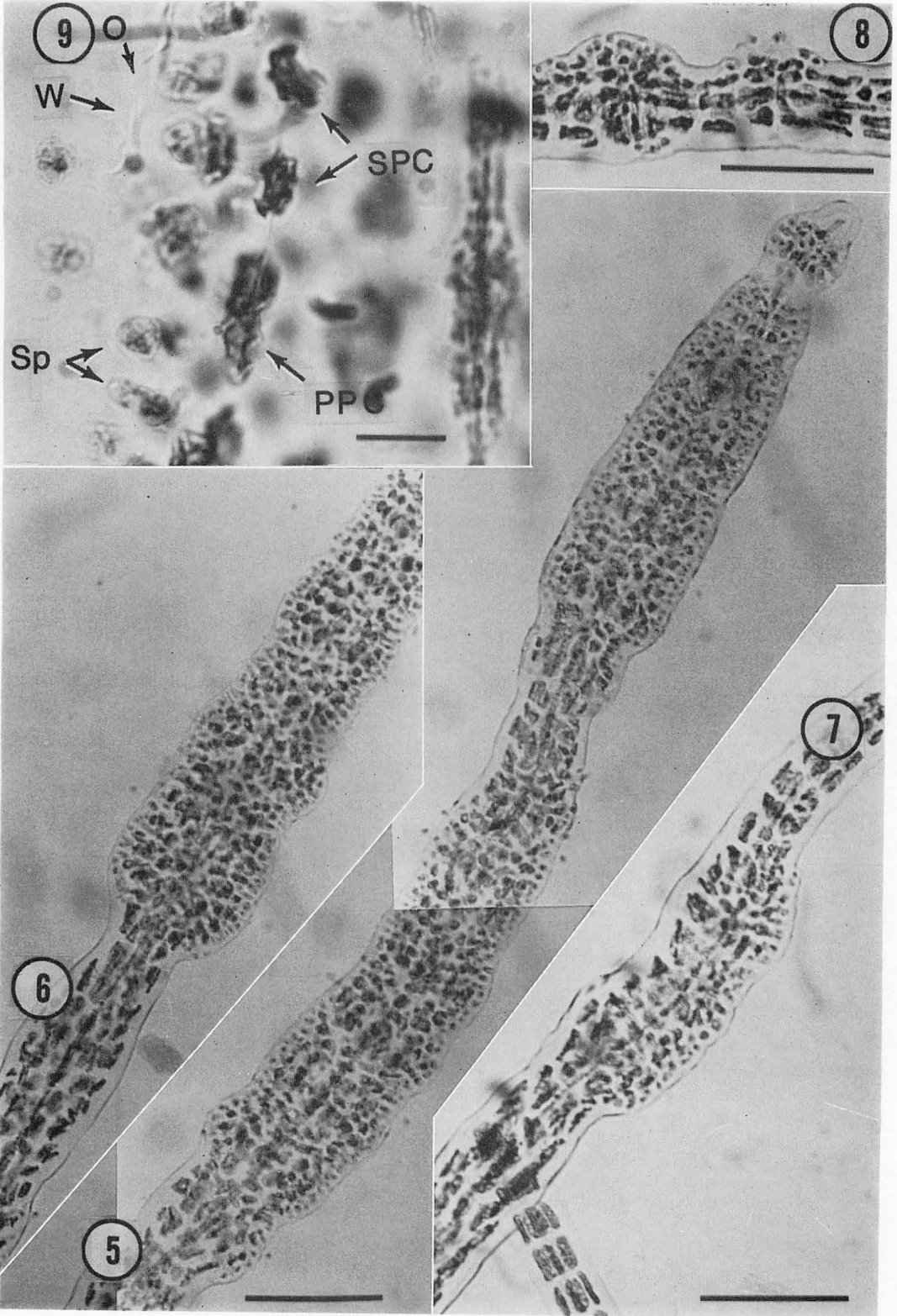
Spermatangia of Bostrychia montagnei.

By the end of the third month in culture, fertile areas developed from newly developed branches as cortical tissues became reproductive (Figs. 1, 2). A greater rate of cell division on ventral (adaxial) sides of fertile areas was evident at the third to fifth axial cells, and resulted in curved branches which frequently rebranched (Figs. 1, 2). Spermatangial areas developed behind a prominent dome-shaped apical cell and a small, plate-like, second axial cell. Frequently by the third axial cell, immature spermatangia were present (Fig. 3). Spermatangial areas extended over as many as 44 axial cells, with $\bar{X}=31.3$ cells ± 8.11 S.D., $n=12$.

Bases of spermatangia were larger than adjoining vegetative areas, and axial cells were shorter cells than cells in vegetative areas ($\bar{X}=31.7$ μm ± 8.06 S.D. for reproductive axial cells versus 53.2 μm ± 14.70 S.D. for vegetative axial cells, $n=12$). Because axial cells were equivalent in width ($\bar{X}=6.1$ μm ± 1.55 S.D. vs. 6.4 μm ± 1.25 S.D., $n=12$, respectively), axial cells in spermatangial areas appeared more



Figures 1 to 4. Male thalli of *Bostrychia montagnei*. Fig. 1. Fertile curved branches of a mature male thallus. Scale bar=250 μ m. Fig. 2. Young male branch showing branching. Scale bar=100 μ m. Fig. 3. Immature spermatangia are present at the third axial cell. Scale bar=10 μ m. Fig. 4. Details of primary parent cell (PPC) and secondary parent cells (SPCs), and spermatia (Sp) focused near the plane of the axial cell. Note empty spermatangium (S) and an opening (O) in the cell wall (W) through which spermatia are released. Scale bar=10 μ m.



prominently than cells in vegetative areas.

From the third and to the end of a spermatangial area, four primary parent cells (=mother cells)¹ were found per axial cell. A primary parent cell (PPC) was adaxially pit-connected to the axial cell, and abaxially pit-connected to two or three secondary parent cells (SPC) (Figs. 4, 10). In contrast to mature ovoid spermatia, parent cells were larger, darkly stained, had dense cytoplasm, and were somewhat star-shaped (Figs. 4, 10). These cells produced multiple spermatia. In several, a third row of cells was also observed to produce multiple spermatia. Empty spermatangia remain after release of spermatia (Fig. 4).

Thus, one PPC produced as many as 19 cells in a dense aggregate, four of which were SPCs, and 15 of which developed into spermatangia. Lengths of parent cells ranged from 5.2 to 9.9 μm on the longer axis, with a mean length, $\bar{X}=7.4 \mu\text{m} \pm 1.61$ S.D., and mean width, $\bar{X}=4.7 \mu\text{m} \pm 0.87$ S.D., $n=12$.

Production of spermatangia was prolific by *B. montagnei*, with every major growing point producing spermatia, including newly developed monosiphonous filaments which were re-growing from an excised end of the main axis. Mature spermatia were nearly ovoid, highly vacuolate cells, each with a single large nucleus (Fig. 4). Sizes of spermatia ranged from 6.4 to 9.9 μm with a mean length, $\bar{X}=6.9 \mu\text{m} \pm 1.47$ S.D. and a mean width, $\bar{X}=4.3 \mu\text{m} \pm 0.76$ S.D., $n=12$. As mature spermatia were released from the overlying cell wall, they lacked conspicuous wings or projections.

¹ The term "mother" in botany is "usually used in the sense of 'parent'" (JACKSON 1928); herein we follow SCHMID (1977) in an effort to avoid inaccuracies and bias in anatomical and morphological terminology.

Spermatangia of Bostrychia binderi.

Fertile areas on branches of *B. binderi* occurred either apically or distally on otherwise unmodified, corticated, vegetative branches, and about half of all fertile branches in this isolate had discontinuous areas of spermatangial production (Figs. 5, 8). One branch for example, had four discrete areas where spermatangia were produced, an apical area and three other spermatangial regions separated by regions of three to as many as nine vegetative axial cells (Fig. 5). Spermatangial production began at the third to the seventh axial cell in apical patch, and continued to as many as the 23rd axial cell. Axial cells in reproductive portions were as long as cells in vegetative branches of similar length (38.1 $\mu\text{m} \pm 3.48$ S.D. versus 39.7 $\mu\text{m} \pm 8.40$ S.D., $n=12$, respectively, Fig. 6). Lateral, partially monosiphonous branchlets never bore spermatangia.

In five fertile branches, spermatangia were produced predominantly on one side for as many as six axial cells (Figs. 7, 8). These asymmetric developments of spermatangia were distal to a branch apex, and were usually less than four axial cell long.

In apical areas, four PPCs were observed, while at distal regions, up to five PPCs were found. A PPC was pit-connected to a SPC which in turn was pit-connected to other SPCs in a uniseriate row; a row was composed of two to three SPCs (Figs. 9, 10). A PPC was larger than SPCs, and ranged in length from 6.4 to 11.6 μm , with a mean length, $\bar{X}=8.6 \mu\text{m} \pm 5.57$ S.D., and a mean width, $\bar{X}=6.3 \mu\text{m} \pm 1.84$ S.D., $n=12$.

One PPC supported as many as 24 cells, 8 SPCs, and 16 developing spermatia. The ovoid spermatia of *B. binderi* ranged in length from 5.2 to 7.5 μm with a mean

Figures 5 to 9. Male thalli of *Bostrychia binderi*. Fig. 5. Fertile portions separated by vegetative cells on a mature branch. Scale bar=100 μm . Fig. 6. Enlarged base of a fertile area. Scale bar=100 μm . Fig. 7. Asymmetric development of a fertile patch on a branch. Scale bar=100 μm . Fig. 8. Asymmetric and disjoint developments of spermatangia on a branch. Scale bar=100 μm . Fig. 9. Details of primary (PPC) and secondary (SPC) spermatangial parent cells and spermatia (Sp) focused on the plane of the axial cell. Note an opening (O) in the cell wall (W) through which spermatia are released. Scale bar=10 μm .

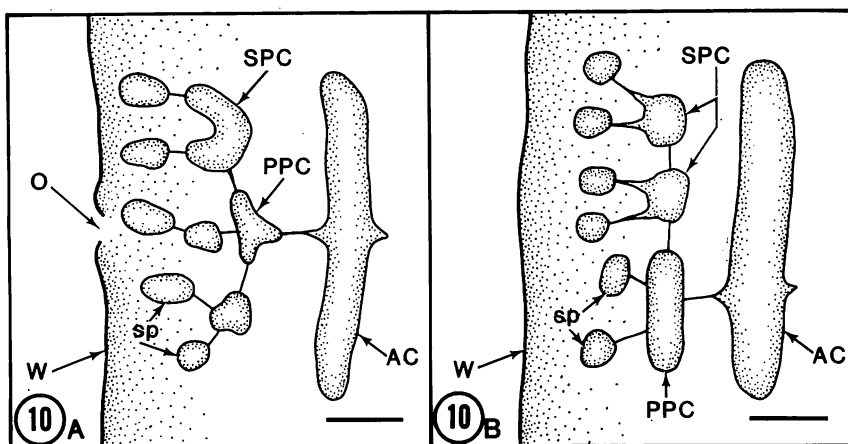


Fig. 10. Comparison of male reproductive structures showing (10A) the branched relationship of a primary parent cell (PPC) to secondary parent cells (SPCs) in a di- or trichotomous arrangement for *B. montagnei*, and (10B) the linear arrangement of a single primary parent cell (PPC) connection to chains of secondary parent cells (SPCs) for *B. binderi*. Scale bar = 10 μm .

length, $\bar{X} = 6.4 \mu\text{m} \pm 0.63 \text{ S.D.}$, and a mean width, $\bar{X} = 4.3 \mu\text{m} \pm 0.63 \text{ S.D.}$, $n = 12$.

Discussion

The goal of this research was to describe spermatangia for two species of *Bostrychia* (sensu Post 1936) which, on vegetative grounds, belong to two species groups (sensu Post 1936). Even though *B. montagnei* and *B. binderi* are not apparently closely allied species, we found that spermatangia developed in ordinary branches, and spermatangia supplanted superficial cortical cells in fertile branches. Both species had similarly sized, ovoid, vacuolate spermatia which lacked the conspicuous wings as seen in *Agloathmion neglectum* (MAGRUDER 1984). Thus, certain characteristics of spermatangial development appear to be conserved in this genus.

However, these species did differ in the shape of thallus branches which bear spermatangia, and details of primary and secondary parent cell arrangements (Table 1). For *B. montagnei*, the tissues which produced spermatangia recurved, and entire branches were dedicated to prolific spermatangial production. For *B. binderi* under

similar growth conditions, there was little modification of polysiphonous vegetative branches which ultimately bore spermatangia. *Bostrychia binderi* had as many as four distinct areas which produced spermatangia on a branch, and some areas developed asymmetric fertile regions. In comparison to *B. montagnei*, spermatangial production by *B. binderi* was less regular, with less differentiation of specialized branches.

Because *B. binderi* was able to produce spermatangia in small, unmodified areas, this species and its close relative *B. tenella* may produce small numbers of spermatangia under a wide range of environmental conditions. In contrast, because whole branches were dedicated to spermatangial production for *B. montagnei*, that species may produce large numbers of spermatangia, infrequently. This hypothesis would help explain why males had not been reported before for *B. montagnei* and why they are rare for its closest relative *B. scorpioides* (PRUD'HOMME VAN REINE and SLUIMAN 1980). By comparison, males for *B. tenella* have been described since 1901 (FALKENBERG 1901).

Other differences existed among these

two species. For *B. montagnei*, a PPC was directly pit-connected to several SPCs in a di- or trichotomy of cells, while for *B. binderi*, a PPC was pit-connected to a uniseriate filament of parent cells, and not directly pit-connected to each parent cell (Figs. 4, 9, 10). Pit-connections of PPC to axial cells were centrally located for *B. montagnei* while somewhat more basally located for *B. binderi* as well as for *B. tenella* as described by FALKENBERG (1901) based on Tongan specimens, not type-locality material.

Comparison of spermatangia of B. montagnei, B. arbuscula and B. scorpioides.

Some similarities exist in the production of spermatangia among *B. montagnei* and its morphologically similar species, *B. arbuscula* and *B. scorpioides*. Similar to *B. montagnei*, spermatangia in *B. arbuscula* and *B. scorpioides* develop in ordinary branches (HOMMERSAND 1963, PRUD'HOMME VAN REINE and SLUIMAN 1980), and spermatangia replace cortical cells in a branch. Spermatangial branches of *B. arbuscula* coil to the ventral side, as a result of the development of a two-layered cortex on the dorsal side of these branches (HOMMERSAND 1963). Spermatangial branches of *B. montagnei* coil to the ventral side because of a multiplication of cells in the existing layer on the dorsal side of a branch. Though no curve is reported in male branches of *B. scorpioides* (PRUD'HOMME VAN REINE and SLUIMAN 1980), those branches studied may have been relatively straight, mature branches which secondarily developed spermatangia. An illustration of mature spermatangial branches for *B. scorpioides* (Fig. 206-E, NEWTON 1931) shows inflated, somewhat curved branches, only slightly similar to those pictured for *B. arbuscula* by HOMMERSAND (Plate 5, HOMMERSAND 1963).

Some of the differences between *B. arbuscula* and *B. montagnei* are found in analysis of fertile branch construction. In *B. arbuscula*, fertile portions are found at the morphological point in a branch where six pericentral cells occurred per axial cell

(Table 1, HOMMERSAND 1963). With continued growth of these branches, the number of pericentral cells reduces to four per axial cell, i.e., the number per axial cell observed here for fertile branches of *B. montagnei*. For *B. arbuscula*, fertile apices cease branching at that time, and tips grow to lengths of 50 or more segments (HOMMERSAND 1963); spermatangia are formed at the sixth or eighth segment behind the apex, and continue for the next 10 to 15 segments; beyond that region, empty spermatangia are found (HOMMERSAND 1963). For *B. montagnei*, we found spermatangia produced at the third axial cell, to at least a length of about 30 segments of fertile tissue. In this species, branching of fertile branches occurred at many stages of spermatangial production.

Mature branches are found to produce spermatangia in *B. scorpioides* (PRUD'HOMME VAN REINE and SLUIMAN 1980), and in NEWTON's (1931) illustration they bear a resemblance to some branches seen here for *B. montagnei*. Further comparisons between *B. montagnei* and *B. scorpioides* are limited (Table 1) because *B. scorpioides* did not produce males in culture (PRUD'HOMME VAN REINE and SLUIMAN 1980).

Bostrychia arbuscula and *B. montagnei* were similar in many aspects of spermatangial tissues. Geographical distributions of these related species, however, does not overlap (Table 1). Supplemental investigations are needed to test if Atlantic isolates of the widespread species *B. scorpioides* and *B. montagnei* are closely related by providing missing details of male development for *B. scorpioides*. These data may also identify interesting population-based differences for Australian individuals of *B. scorpioides*, and help clarify the relation between *B. arbuscula* and *B. montagnei*.

Comparison of spermatangia of B. binderi, B. tenella and B. calliptera.

FALKENBERG's illustration of a cross-section through male tissues of *B. tenella* from the south Pacific island of Tonga (Fig. 11, FALKENBERG 1901) shows a very similar

Table 1. Comparison of vegetative morphology, spermatangial characteristics and distribution for species of *Bostrychia* where spermatangia have been described.

Species	MORPHOLOGY		DISTRIBUTION
	Vegetative	Spermatial	Type locality & Range
<i>B. arbuscula</i>	several layers cort ¹ haptera: no ax habit: flattened	4 to 6 pc/ax ² 6 to 50 segs ? spc/ax 3 sp/spc ventral diff	Otago, New Zealand ^{1,2} endemic to New Zealand
<i>B. montagnei</i>	several layers (<7) cort ¹ haptera: no ax habit: radial	4 pc/ax 3 to >44 segs 16 to 20 spc/ax 2 to 3 sp/spc ventral diff	Key West, Florida ^{3,4} Caribbean, W Africa
<i>B. scorpioides</i>	1 to 2 layer cort ¹ haptera: no ax habit: distichous branching	6 (?) pc/ax ^{5,10} ? segs ? spc/ax 2 to 3 sp/spc no ventral diff	Selsey, England ^{3,4,5} Australia, So. Africa Europe, New Zealand S America,
<i>B. binderi</i>	1 to 3 layers ^{1,3} haptera: no ax habit: tripinnate branching	4 to 5 pc/ax 1 to 23 segs 12 to 45 spc/ax 3 to 4 sp/spc no ventral diff	Durban, So. Africa ¹ Caribbean, S America Indian, Australia W tropical Pacific
<i>B. tenella</i>	1 to 3 layers cort ^{1,9} haptera: no ax habit: distichous branching	4 (?) pc/ax ⁸ 8 to ? segs ? spc/ax 2 (?) sp/spc no ventral diff	Christiansted, St. Croix ^{1,9} Caribbean, Africa Indian, China W tropical Pacific
<i>B. kelanensis</i>	no cort ¹ haptera: w/ ax habit: short branches	5 to 6 pc/ax ⁶ 6 to 26 segs 14 to 19 spc/ax 1 to 2 sp/spc diff not noted	Kelana, New Guinea ¹ India, Sumatra Australia
<i>B. pinnata</i>	no cort ^{6,7} haptera: w/ ax habit: pinnate branching	5 pc/ax ⁷ 9 to 15 segs 40 to 60 spc/ax 1 to 4 sp/spc ventral diff	Okinawa, Japan ^{6,7} Japan, Australia

Key to Terms: ax=axial cell; segs=length of fertile area in numbers of axial cells; cort=cortication; diff=fertile branch differentiation; pc=pericentral cell; spc=spermatangial parent cell; sp=spermatium (a).

References: ¹POST 1936; ²HOMMERSAND 1963; ³TAYLOR 1960; ⁴SLUIMAN 1979; ⁵PRUD'HOMME VAN REINE and SLUIMAN 1980; ⁶TANAKA and CHIHARA 1984a; ⁷KING and PUTTOCK 1986; ⁸FALKENBERG 1901; ⁹BØRGESEN 1918; ¹⁰NEWTON 1931.

shape of spermatangial branches and arrangement of primary and secondary parent cells as reported here for *B. binderi*. FALKENBERG depicts a PPC pit-connected to the base of an axial cell, which in turn is pit-

connected to a SPC. Both types of parent cells have two associated spermatangia. For *B. binderi*, two or more SPCs were pit-connected in a row (Fig. 10B) with one or more rows of SPCs pit-connected to a single

primary parent cell. Primary parent cells were typically pit-connected near the base of axial cells. For *B. binderi*, no PPC was observed producing spermatangia, while for *B. tenella*, our interpretation of FALKENBERG's illustration suggests that spermatangia are produced by PPC. In contrast with two or more SPCs observed here for *B. binderi*, *B. tenella* (FALKENBERG 1901) had only one SPC attached to each PPC.

Bostrychia tenella and *B. binderi* are pantropical (Table 1), with nearly complete overlap in distribution, and vegetative habit (POST 1936, TSENG 1943). While these species are similar in details of construction of spermatangial tissues, how much these details may vary with biogeographical distribution is unknown. Comparisons with the other species of this subgeneric group such as *B. calliptera*, are not possible because no description for its males exists. Descriptions of males from Pacific and Atlantic populations of *B. calliptera* might help test recognition of this group.

Among related species of *Bostrychia*, there are distinctions in the spermatangial developmental processes. Comparisons with details of males for other, less related species, *B. kelanensis* GRUNOW (TANAKA and CHIHARA 1984b), and *B. pinnata* TANAKA et CHIHARA (KING and PUTTOCK 1986), demonstrate that numbers of pericentral cells per axial cell, numbers of fertile segments, as well as spermatangial parent cells per axial cell differ (Table 1).

Comparison of spermatangia among genera.

A comparison of spermatangial tissues among genera of the Rhodomelaceae demonstrates that *Bostrychia* has the least complex spermatangia. Spermatangia of *Murrayella* SCHMITZ and some species of *Polysiphonia* GREV. are strikingly similar in gross morphology to those of *B. binderi* and *B. tenella* (GRUBB 1924; APONTE and BALANTINE 1987). In contrast, many genera have highly modified spermatangia, such as those derived from trichoblasts for some species of *Herposiphonia* NÄEGLI (BØRGESEN

1918; NORRIS and BUCHER 1982) and *Polysiphonia* GREV. (BØRGESEN 1918), conceptacle-like terminal pockets in branchlets of *Laurencia* LAMOUR. (SAITO 1967), kidney-shaped appendages for *Digenia* C. AG. (BØRGESEN 1920), or plate-like forms for *Chondria* C. AG. and *Acanthophora* LAMOUR. (BØRGESEN 1918). These comparisons suggest that based on anatomy of spermatangial tissues, *Bostrychia* is a relatively primitive genus in the Rhodomelaceae, as suggested by HOMMERSAND (1963).

For species of *Bostrychia*, these studies show the details of spermatangial development, reveal similarities and differences between different subgeneric groups associated on vegetative grounds. Additionally, comparison with other genera in the Rhodomelaceae suggests that *Bostrychia* is a primitive genus of relatively simple, undifferentiated reproductive structures.

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Celia M. SMITH*, & James N. NORRIS:** カリブ海産 *Bostrychia montagnei* HARVEY と *B. binderi* HARVEY (フジマツモ科, イギス目) における精子嚢の存在と構造

表記の2種を培養した結果, それぞれ精子嚢の発達の様子が異なることが分かった。

B. montagnei の雄株では, 精子嚢は3番目から少なくとも44番目までの中軸細胞から形成される。カーブした成熟した枝の中軸細胞1細胞当たり, 4個の精子嚢の親細胞が生じる。それぞれの精子嚢の1次親細胞 (PPC) は, 精子嚢を造る少なくとも3個の2次親細胞 (SPC) とピット・コネクションで連絡する。1次親細胞 (PPC) は, 15細胞が集合しており, 内4細胞が2次親細胞 (SPC), 15細胞が不撻または撻性のある精子嚢である。

B. binderi の雄株では, 精子嚢は2番目から少なくとも23番目までの中軸細胞から形成される。真っ直ぐの成熟した枝の中軸細胞1細胞当たり, 4-5個の精子嚢の親細胞が生じる。それぞれの精子嚢の1次親細胞 (PPC) は, 1個の2次親細胞 (SPC) と, 更に順に2個の2次親細胞と, 1列に連絡している。1次親細胞 (PPC) は, 24細胞が集合しており, 内8細胞が2次親細胞 (SPC), 16細胞が精子嚢である。 (*Department of Botany, National Museum of Natural History, Smithsonian Institution, **Department of Botany, University of Hawaii)