A comparative study of spermatangia in *Bostrychia* Montagne (Rhodomelaceae, Rhodophyta)

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The structure of the spermatangial stichidia in seven species of *Bostrychia* Montagne is examined, and shown to be referable to the basic structure of the vegetative axis of each species. The variation shown in the arrangement of cortical cells in the stichidia is far greater than anticipated from published information, and adds little to an understanding of relationships within the genus.

Key Index Words: Bostrychia—*Rhodomelaceae*—*Rhodophyta*—*spermatangia*—*systematics*—*taxonomy*.

The Bostrychioideae is a well defined subfamily within the Rhodomelaceae, and following Post (1936) all members of the subfamily have been placed in the single genus *Bostrychia* Montagne. In a world-wide revision of the group, King and Puttock (1989) challenged this view. The genus *Bostrychia* was maintained for the eleven species in which there are two tiers of pericentral cells per axial cell, and in which cortication (when present) of the first formed pericentral tier is completed before cortication of the second pericentral tier. The genus *Stictosiphonia* J. D. Hooker et Harvey was resurrected and emended for six species with 3–5 tiers of pericentral cells per axial cell, and in which the cortication of the second and subsequent pericentral cells takes place prior to the formation of the second tier of cortical cells. The two genera, *Stictosiphonia* and *Bostrychia*, had already been recognized as subgenera by Falkenberg (1901) on the basis of the number of tiers of pericentral cells alone.

The taxonomy of the Bostrychioideae has been, and continues to be, based essentially on vegetative structures, a fact attributed to the comparative rarity of reproductive material. Smith and Norris (1988a) investigated the structure of spermatangia in cultured material of two taxa of *Bostrychia* (*B. montagnei* Har-

vey and *B. binderi* Harvey), and compared their observations with published information on supposedly related species. In the present paper we have made original observations on spermatangial plants of seven of the 11 species that we recognize in *Bostrychia*, and interpreted these in the light of our recent study of relationships in the genus.

Any comparative study of the development of the spermatangial stichidia in *Bostrychia* requires the careful application of terminology. Tanaka (1989) introduced the term "spermatangial stichidia" for the reproductive portion of what have been referred to as spermatangial branches (King and Puttock 1989) and this term is adopted here. Smith and Norris (1988a) introduced the terms "adaxial pit connection" for the attachment of the proximal pericentral cell to the axial cell, and "abaxial pit connection" for its attachment to the distal pericentral cell or any subsequently formed cortical cells but this is unwarranted and confusing since the latter is only rarely in a strictly abaxial position. In the Rhodomelaceae the terms dorsal and ventral refer to the cell row derived from the first and last formed pericentral cells respectively, and not simply the upper and lower side. In lateral branches, the ventral cells will be in the adaxial position and the

dorsal side will be then directed away from the axis. This results in the determinate lateral branches growing towards the indeterminate main axis rather than towards the substratum, as do the indeterminate branches.

Spermatogenous cells are not markedly differentiated from normal vegetative cells and any superficial cell can be reproductive. All cells in a spermatangial stichidium, with the exception of the axial cells, appear able to produce spermatia. Referring to the initial pericentral cells as primary parent (mother) cells which later divide to become secondary parent cells (Tanaka 1989), or referring to the proximal pericentral cell as a primary parent cell, and other corticating cells as secondary parent cells (Smith and Norris 1988a) is unnecessary since the development is essentially that in the vegetative axis and therefore there is no need to create a separate terminology.

Materials and Methods

Observations of the spermatangial stichidia of the male gametophytes of seven species of *Bostrychia* were made on permanent microscope slides held at UNSW (John T. Waterhouse Herbarium at the University of New South Wales) and LTB (Latrobe University, Melbourne), and on slides prepared from dried and pickled field collected herbarium specimens. *Bostrychia tenella* included material formerly referred to *B. binderi* Harvey. Spermatangial stichidia were analyzed for the spatial position and attachment of every cell over four consecutive axial cells. Four stichidia were examined for each species. It is virtually impossible to trace the cellular connections of all cells on mature spermatia-bearing stichidia because of the density of cells present at that stage. Therefore, since the stichidia are not secondarily reproductive, "spent" stichidia were used. Apart from these stichidia being easier to interpret, they are necessarily fully developed.

The material was examined to determine whether there is a dorsiventral bias in cell production (i.e. a diminution of cortical development from the first to last formed

pericentral cell in the typical Rhodomelacean sequence); whether the dorsal cell row is in the lateral abaxial position of the branches as predicted by the arrangement of cells at the branch initiation; whether the proximal pericentral cell is more highly corticated than the distal pericentral cell ; and whether the cortication of the spermatangial stichidia reflects the degree of cortication of the vegetative axes.

Specimens examined:

Bostrychia montagnei Harvey—Key West, Florida, U.S.A., Harvey (syntype MEL 672268).

Bostrychia moritziana (Sonder ex Kuezting) J. Agardh—Daintree R. crossing, Qld, Australia, 16°15′S 145°23′E, 8.vii.1984, King and Puttock UNSW 16835.

Bostrychia pilulifera Montagne—Ilha de Marca, estado do Amapa', Brazil, 21.x.1988, de Paula SPF 54065 (UNSW).

Bostrychia pinnata J. Tanaka et Chihara— Daintree R. crossing, Qld, Australia, 16°15′S 145°23′E, 8.vii.1984, King and Puttock UNSW 16834; Cairns International Airport Road, Cairns, Qld, Australia, 16°52′S 145°45′E, 7.vii.1984, King and Puttock UNSW 16836.

Bostrychia radicans (Montagne) Montagne—Rapid Ck, Darwin, N. T., Australia, 12°27′S 130°50′E, 4.xii.1985, Kilkeary UNSW 18148.

Bostrychia tenella (Lamouroux) J. Agardh—Ellis Beach, Cairns, Qld, Australia, May (NSW 126959); Red Beach, Weipa, Qld, Australia, 12°35′S 142°52′E, 22.vii.1984, King and Puttock UNSW 17025.

Bostrychia tenuissima R. J. King et Puttock—Arno Bay, Victoria, Australia, 16.iii.1981, Woelkerling (LTB 12237, LTB 12341).

Results

Spermatangial parent cells in spermatangial stichidia

The number of cortical cells connected to distal and proximal pericentral cells were scored in sequence for each of four axial

Table 1. Cortical production per axial cell in seven species of *Bostrychia*. The values are means based on four consecutive axial cells in each of four spermatangial stichidia. The range shows the variation observed in the four separate stichidia (except for *B. radicans* where only one stichidium was available). The number of pericentral cells around the axis is not constant, and the number of cells on which the average is based is indicated [#].

Species	dorsal	subdorsal	subdorsal	subventral	ventral
B. montagnei	5.7 (4.5–7.5) [16]	4.4 (3.5–5.5) [16]	3.0 (2.3–4.3) [16]	2.5 (1.5–3.5) [16]	1.9 (1.5–2.3) [13]*
B. moritziana	0.9 (0–2) [16]	0.3 (0–1.3) [16]	0** [16]	0** [16]	0** [2]
B. pilulifera	9.7 (8.3–12) [16]	8.3 (6.8–9) [16]	7.3 (6.8–8.5) [16]	6.6 (5.8–7.5) [16]	5.3 (4.8–6) [15]
B. pinnata	3.8 (2.5–5.3) [16]	3.4 (1.8–4.5) [16]	2.7 (1.8–3.8) [16]	2.1 (1.3–3.5) [16]	1.9 (0.5–3.3) [16]
B. radicans	3.5 [4]	3.3 [4]	n/a —	2 [4]	2 [4]
B. tenella	5.2 (4.3–6.5) [16]	3.7 (1.8–6.5) [16]	3.7 (2–5.8) [16]	3.7 (2.3–5.5) [16]	2.9 (1–5.3) [16]
B. tenuissima	10.3 (9–11.8) [16]	7.7 (6.8–8.5) [16]	5.3 (4.8–6) [16]	4.3 (3.3–5.3) [16]	3 (2.3–3.8) [12]

* In one case *Bostrychia montagnei* had a single axial cell with 6 rather than 5 pericentral cells around the axis.

** In *Bostrychia moritziana* the development of the pericentral cells in the spermatangial stichidium is incomplete in the ventral position. In none of the material observed were pericentral cells other than those in two dorsal cell rows further corticated.

segments in a single spermatangial stichidium, and this was repeated for four stichidia. The number of cortical cells attached to a particular pericentral cell is affected by the spatial arrangement of neighbouring cells. The sequence of production of pericentral cells in the vegetative indeterminate axis of the Rhodomelaceae follows a set pattern (Parsons 1975). In corticate species of *Bostrychia* the cortical productivity of the dorsal cell row in vegetative material is higher than that of the ventral. In species in which the spermatangial stichidium is developed on polysiphonous or corticated axes the number of potentially spermatogenous cells in the dorsal cell row is highest, and lowest in the ventral row. In those few cases where the spermatangial stichidium can be developed on monosiphonous axes (*Bostrychia moritziana*, and in *B. tenella*—see Tanaka, 1989) the data are based on the presumption that the most productive cell row is the dorsal cell row. The extent of cortication from the dorsal to the ventral cell rows is presented in Table 1. The pattern in which these numbers of corti-

cal cells can be derived from the basic axial cell/pericentral cell arrangement is indicated in Figure 1. In this schematic diagram the diversity found in each species is indicated.

The dorsal cell row in a spermatangial stichidium occurs in the abaxial position in relation to the main axis. As a consequence the spermatangial stichidia of all species examined, with the exception of those in *Bostrychia moritziana*, are curved towards the apex of the indeterminate branch from which they are derived.

Cortication of distal/proximal tiers of pericentral cells

According to King and Puttock (1989) the pattern of cortication of the pericentral cells in the spermatangial stichidia of *Bostrychia* can be interpreted as conforming to the same basic pattern as in the vegetative thallus. That is, it favours the completion of cortication of the proximal pericentral cell before that of the distal pericentral cell of an axial cell. The number of cortical cells arising from the proximal pericentral cells is compared with the number arising from distal pericentral cells in
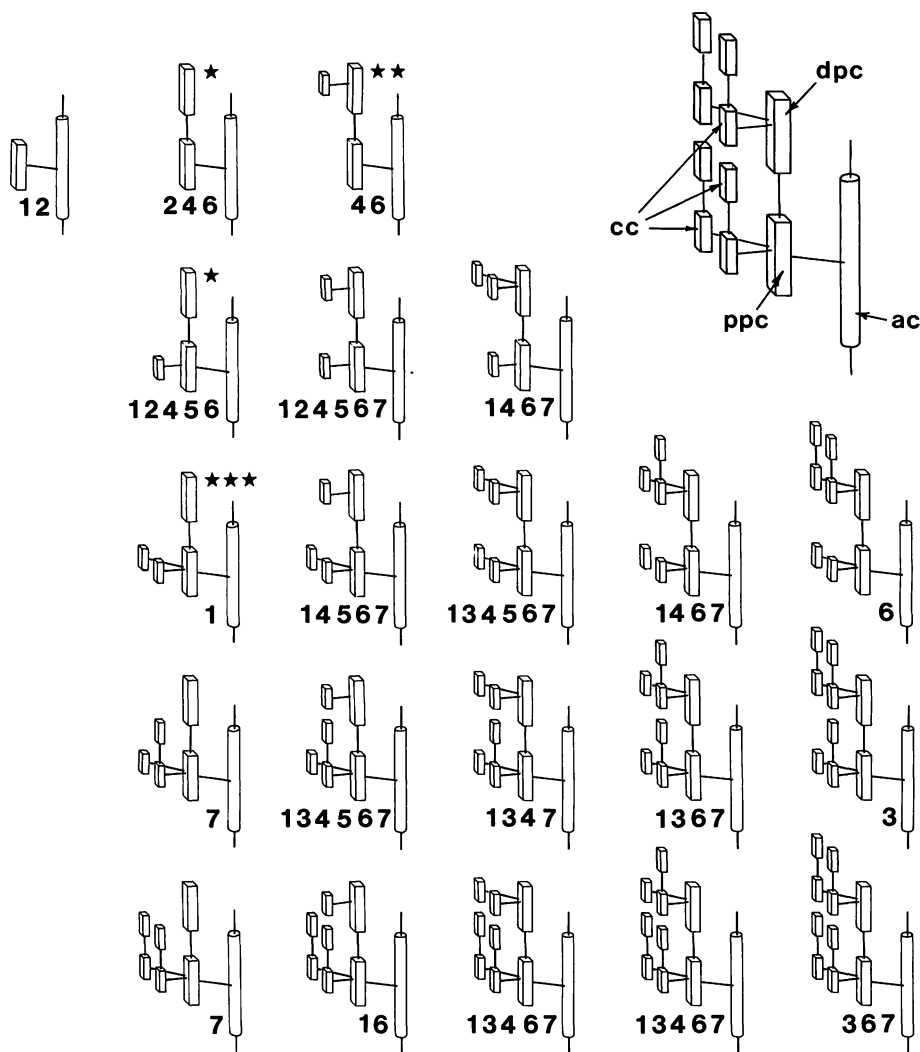
Fig. 1.   Patterns of cortical development observed in the spermatangial stichidia of *Bostrychia* [1 = *B. montagnei*; 2 = *B. moritziana*; 3 = *B. pilulifera*; 4 = *B. pinnata*; 5 = *B. radicans*; 6 = *B. tenella*; 7 = *B. tenuissima*].   The series illustrates the observed arrangements of the axial cell (ac), the proximal pericentral cell (ppc), the distal pericentral cell (dpc), and the primary cortical cells (cc).   The table would be extended to the bottom and right to accommodate a third primary cortical row on the proximal pericentral cell, or a secondary cortical cell layer on the primary cortical cells.   The patterns of development illustrated by Tanaka (1989) for *B. tenella**, and by Smith and Norris (1988a) for *B. binderi* (= *B. tenella*)** and *B. montagnei**** are indicated on the diagram.

Table 2.
Cortication of vegetative axes and spermatangial stichidia

The cortication observed in the vegetative axes and the spermatangial stichidia shows that there is little consistency between the amount of cortical development in the spermatangial stichidia and the vegetative thallus (Table 3).   The values include the pericentral layer and therefore cannot be directly compared with values in King and Puttock (1989).

Discussion

Several recent papers have addressed aspects of the reproductive biology of *Bostrychia* species (Smith and Norris 1988a, b; Kumano

Table 2. Numbers of cortical cells arising from distal and proximal pericentral cells in seven species of *Bostrychia*. The values are means based on all cells derived from the pericentral cells produced by four consecutive axial cells, in each of four spermatangial stichidia. The range shows the variation observed in four separate stichidia (except in the case of *B. radicans* for which only one stichidium was scored).

Species	Numbers of proximal pericentral cells	Number of distal pericentral cells	Ratio of proximal to distal cell numbers
B. montagnei	2.3 (2.0–2.6)	1.4 (1.1–1.7)	0.6
B. moritziana	0.2 (0–0.5)	0.1 (0–0.3)	0.5
B. pilulifera	4.3 (4.0–4.6)	3.0 (2.2–3.5)	0.7
B. pinnata	1.8 (1.0–2.8)	1.1 (0.7–1.4)	0.6
B. radicans	1.6	1.2	0.8
B. tenella	2.3 (1.2–3.0)	1.6 (1.0–3.0)	0.7
B. tenuissima	3.8 (3.3–4.5)	2.7 (2.3–3.1)	0.7

1988; West and Calumpong 1988; Tanaka 1989). The results presented here are discussed in relation to data on the male gametangial structures in these papers, and in the monograph of the genus (King and Puttock 1989).

In the gametangial stichidia of all seven species of *Bostrychia* examined the dorsal pericentral cells were always more highly corticated than those of the ventral pericentral cells (Table 1). This can be taken as an indication that all species maintain the dorsiventral nature typical of all Rhodomelaceae even in the spermatangial stichidia. It also emphasises the unspecialized nature of the reproductive branches (Hommersand 1963; Smith and Norris 1988a). In those species where the development can be traced from the apex a greater number of cortical cells is observed in the abaxial position and the curvature of the branch is towards the apex of the indeterminate branch from which it diverged. This interpretation differs from that of Smith and Norris (1988a) who considered that curved branches resulted from a greater rate of cell division on the ventral (adaxial) sides of the fertile areas. Smith and Norris (1988a) quoted Prud'homme van Reine and Sluiman (1980) as not reporting curvature of the spermatangial branches of *Bostrychia scorpioides* and suggested that this might be attributed to 'secondarily developed spermatangia' on relatively straight, mature branches. Secondary development of this type has, however, never been shown in any *Bostrychia* species. Furthermore the photograph of the spermatangial branches of *Bostrychia scorpioides* in Prud'homme van Reine and Sluiman (1980)

Table 3. Comparison of cortication of vegetative axes and spermatangial stichidia. The number of cell layers surrounding the axis, including the pericentral layer and the number of pericentral cells around the axis is given.

Species	vegetative cortication				reproductive cort'n	
	indeterminate axis		determinate axis		stichidia	
	number	pericentral cells	number	pericentral cells	number	pericentral cells
B. montagnei	3–5	5–7	0–3	0, 4–6	(1–)2	(4–)5(–6)
B. moritziana	1	5	0–1	0, 4–5	1(–2)	4(–5)
B. pilulifera	3–4	7–8	1–3	6–7	2(–3)	(4–)5
B. pinnata	1	6(–8)	1	4	2	(4–)5
B. radicans	1	7–8	1	5–6	2	4
B. tenella	(1) 2–4	5–7	0–3	0, 4–6	1–2	(4–)5
B. tenuissima	1	5–7	1	5–6	2(–3)	(4–)5

clearly shows the stichidia to curve towards the indeterminate axis.

In the species of *Bostrychia* examined the proximal pericentral cell in the spermatangial stichidium is always more highly corticated than the distal pericentral cell (Table 2), thus indicating for *Bostrychia* the tendency to fill up the cortication of the proximal pericentral cell before the distal cell. These cortical cells, when not forming a complete cortical layer, will be cut off posteriorly (away from the branch apex), laterally, or in the case of the distal pericentral cell, anteriorly, thus giving the appearance of the pit connection to the axis from a medial cell in *B. montagnei* (ditrichotomous arrangement, Smith and Norris 1988a: fig. 10A) or the distal of three in *B. binderi* (linear arrangement, Smith and Norris 1988a: fig. 10B) or both conditions from the same axial cell in *B. tenella* (Tanaka 1989: fig. 15). Our interpretation of these conditions is indicated in Figure 1.

In both the paper of Smith and Norris (1988a) and that of Tanaka (1989) the patterns of development illustrated do not encompass the wide variation which can be observed in individual species (Fig. 1).

Variation is shown in the number of cortical cells and their arrangement in the spermatangial stichidium. The cultivated material of *Bostrychia montagnei* described by Smith and Norris (1988a) has only partial branches developed into spermatangial stichidia, as is found in some ecological forms of *B. tenella*. This stands in contrast to the situation in the syntype material of *B. montagnei*, which is male, though this was not observed by Harvey (1853). In *B. tenella* at least, spermatangial stichidia can be borne on either monosiphonous or polysiphonous branches (see below).

The degree of cortication shown in the spermatangial branches bears no direct relationship with that of the vegetative thallus (Table 3). However, in the species with monosiphonous ultimate branches examined (*Bostrychia montagnei*, *B. moritziana* and *B. tenella*), the lowest numbers of cortical cells in the spermatangial stichidia are recorded.

The pattern of reproductive development on unspecialized branches that we have observed in the spermatangial stichidia is also apparent in the development of tetrasporangial and procarpial stichidia of the Bostrychioideae.

The only published case in which the spermatangial stichidia do not conform to the pattern of development described here is that in which Kumano (1988) reported both male and female organs on 'monoecious' *Bostrychia flagellifera* Post. On the basis of the illustration in that paper we would question the assignment of the specimen to *B. flagellifera* (= *B. tenella* ssp. *flagellifera* (Post) R. J. King et Puttock). In Kumano (1988, figure 2) more cortical cells are shown arising from the proximal pericentral cell than we have observed even in the most robust forms of *B. tenella*. The spermatangial branch illustrated bears a superficial resemblence to an epiphyte, but is less well developed than the alloparasite *Dawsoniocolax bostrychiae* originally described from Brazil by Joly and Yamaguishi-Tomita (1967, 1969).

Kumano (1988) is the only report of monoecious plants from field collected material. However, gametophytic plants are rarely encountered in nature and recently published observations on gametophytic stages are based on plants grown in culture (Smith and Norris 1988a, b; West and Calumpong 1988). Cultured plants may behave atypically as is seen in the mixed phase plants reported by West and Calumpong (1988).

The table prepared by Smith and Norris (1988a) comparing the vegetative morphology and spermatangia in *Bostrychia* presents a number of problems. Firstly two of the species included, *B. arbuscula* J. D. Hooker et Harvey and *B. kelanensis* Grunow ex Post, would now be placed in the genus *Stictosiphonia* (King and Puttock 1989) and another two, *Bostrychia tenella* and *B. binderi*, are considered to be synonymous (King *et al.* 1988). In the present study the data for *B. tenella* are based on two stichidia from material of *B. tenella sensu* Post (1936) and two from the ecological form previously known as *B. binderi*. The stichidia were

borne on polysiphonous axes, as was also the case in the material of *B. binderi* of Smith and Norris (1988a). They may also be borne on monosiphonous laterals (West and Calumpong 1988; Tanaka 1989). Further the circumscription of *B. scorpioides* (Hudson) Montagne does not include southern hemisphere specimens which are referred to *B. harveyi* Montagne (King and Puttock 1989). These factors, coupled with an interpretation of phylogeny in the genus based on Post (1936), make it difficult to reconcile the conclusion of Smith and Norris (1988a) that their work "indicates that male thalli are not only useful to the taxonomy of *Bostrychia*, but represent phylogenetic markers for the family Rhodomelaceae" with data now available.

In a major study on the '*Bostrychia-Caloglossa*-Assoziation', Post (1936) revised the genus *Bostrychia*. Post rejected all previous systematic classifications within the genus, but nonetheless supported the taxonomic conclusions reached earlier by Falkenberg (1901). In a brief discussion on systematics in the genus, Post (1936) made the unsupported assertion that the most valuable systematic characteristic is not the number of tiers of pericentral cells. Post made no further comment on the systematics *per se*, but did note that the species of *Bostrychia sens. lat.* (including *Stictosiphonia*) could most easily be separated on the basis of the development of the haptera. Two groups of species were recognized: the 'Ramifulcratae' (with cladohaptera) and the 'Flagellifulcratae' (with peripherohaptera). If this division was considered to be more than simply useful for identification, then it would require a major reassessment of species in the genus. On the basis of detailed studies on vegetative material of all species in the genus including a cladistic analysis, King and Puttock (1989) reiterated the systematic value of the number of tiers of pericentral cells arising from each axial cell (cf. Falkenberg 1901). Furthermore, since the cladohaptera possessed by *Bostrychia radicans* and *Stictosiphonia kelanensis* (Post) R. J. King et Puttock have been shown to be non-homologous structures (King and Puttock 1989) the type of hapteron

has questionable value in an assessment of any relationships.

In recent papers Smith and Norris (1988a, b) have attributed systematic meaning to further characters used in the key to the genus *Bostrychia* in Post (1936). There is, however, no reason why one should consider the key as a systematic arrangement producing groups and subgroups of related taxa. Post's understanding of systematics is interesting, particularly when considering her expectation of yet undiscovered species which would complete various permutations of character states (see table in Post 1939). Such expectations could be considered an extension of her belief that some species were related by neoteny so that species with monosiphony were considered to be development-arrested states of the completely polysiphonous species.

The supposition of Smith and Norris (1988a, b) that *Bostrychia arbuscula*, *B. montagnei* and *B. scorpioides* form a subgroup of closely related species, recognized by Post (1936), is therefore unjustified. Likewise a subgroup consisting of *B. calliptera* (Montagne) Montagne, *B. binderi* and *B. tenella* cannot be maintained as related species. The two characters, extent of cortication and differentiation of the thallus into long and short shoots, listed as separating *B. binderi*, *B. tenella*, *B. calliptera* from the subgroup containing *B. arbuscula*, *B. montagnei* and *B. scorpioides*, have been shown to be of little or no systematic value (King and Puttock 1989) and the continued separation of *B. binderi* from *B. tenella* (and *B. flagellifera*) is unwarranted (King et al. 1988).

The seven species examined in the study represent all five of the informal alliances proposed by King and Puttock (1989); the 'radicans' and tenella' groups are represented by two species each. The tenella group is represented by two corticate species, *Bostrychia tenella* and *B. montagnei* with similar spermatangial stichidia cortication production, consistent with cortication in the vegetative thallus (King and Puttock 1989). The two species in the radicans group (*B. radicans* and *B. pilulifera*) differ in the degree of cortication,

which is consistent with the cortication in the vegetative thallus of *B. pilulifera* and the lack of cortication in *B. radicans*. Both species have prolonged stichidial growth with the subapical 3-12 cells fertile and a long series of spent cells behind them. In all other species the stichidia appear to be simultaneously productive, i.e. the stichidia are either completely fertile or completely empty of spermatia, and this has been confirmed in culture for *B. tenella* by West and Calumpong (1988). The data presented here also support an affinity between the tenella and moritziana groups. The tenella and moritziana groups differ in the type of hapteron although the cladistic analysis places them near each other (King and Puttock 1989).

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R. J. King・C. F. Puttock：紅藻フジマツモ科コケモドキ属の不動精子器に関する比較研究

コケモドキ属 (*Bostrychia*) の7種について不動精子器の四分胞子托の構造を調べた結果，それが各々の種の栄養体の軸の基本構造に関連していることが明らかになった。四分胞子托の皮層細胞の配列にみられる変異は，これまでの報告から予測されるより遙かに大きく，この属内における相互関連の理解に役立つものはほとんどなかった。(School of Biological Science, University of New South Wales, P. O. Box 1, Kensington 2033, Australia)