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# The morphology of *Bostrychia pilulifera* Montagne (Rhodomelaceae, Rhodophyta)

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The vegetative morphology and all reproductive stages of *Bostrychia pilulifera* Montagne (Rhodomelaceae, Rhodophyta) are described in detail from recent collections in Brazil. The relationship of *B. pilulifera* to other species in the genus is discussed.

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

In a worldwide taxonomic revision of the genus *Bostrychia* Montagne, King and Puttock (1989) recognized 11 species, but noted that those species restricted to tropical and southern America, *B. calliptera* (Montagne) Montagne, *B. montagnei* Harvey and *B. pilulifera* Montagne, were known from relatively few collections. In consequence only short diagnoses of these species were provided and reproductive stages were not described in detail. Collections of *B. pilulifera* from Brazil, including fertile material of all stages, have now become available (Paula *et al.* in press). The present paper brings the description of *Bostrychia pilulifera* into line with those provided for other species in King and Puttock (1989), and makes further comments on the relationships of *B. pilulifera* to other species of *Bostrychia*. In spite of the limited material available to King and Puttock (1989) the diagnosis of the species remains essentially unchanged and it can be identified without difficulty using the keys in that paper.

## Materials and Methods

Collections were fixed in formalin-seawater. Specimens were stained in toluidine blue and mounted on microscope slides in karo solution. A representative collection of microscope slides has been deposited in the John T. Waterhouse Herbarium (UNSW). Measurements quoted for cell dimensions include cell walls, as in most preparations some plasmolysis of the protoplast occurred in processing. All drawings were made by C.F.P. with the aid of a camera lucida and light micrographs taken on an Orthoplan photomicroscope (Ernst Leitz Wetzlar GmbH, FRG) using Kodak technical pan 2415 rated at 50 ASA.

## Taxonomy

*Bostrychia pilulifera* was described from material originally confused by Montagne (1840) with *Rhodomela floccosa* (Esper) C. Agardh.

***Bostrychia pilulifera*** Montagne 1842: 252. Syntypes: Cayenne, French Guiana, *Leprieur 349 and Montagne.* Surinam, *Splitgerber 1316/1317.*

*Literature*: Montagne 1850: 286. Kützing 1865: 7, pl. 18 fig. e-h. Post 1936: 20. King and Puttock 1989: 28. Paula *et al.* in press.

*Synonymy*: *Helicothamnion piluliferum* (Mon-

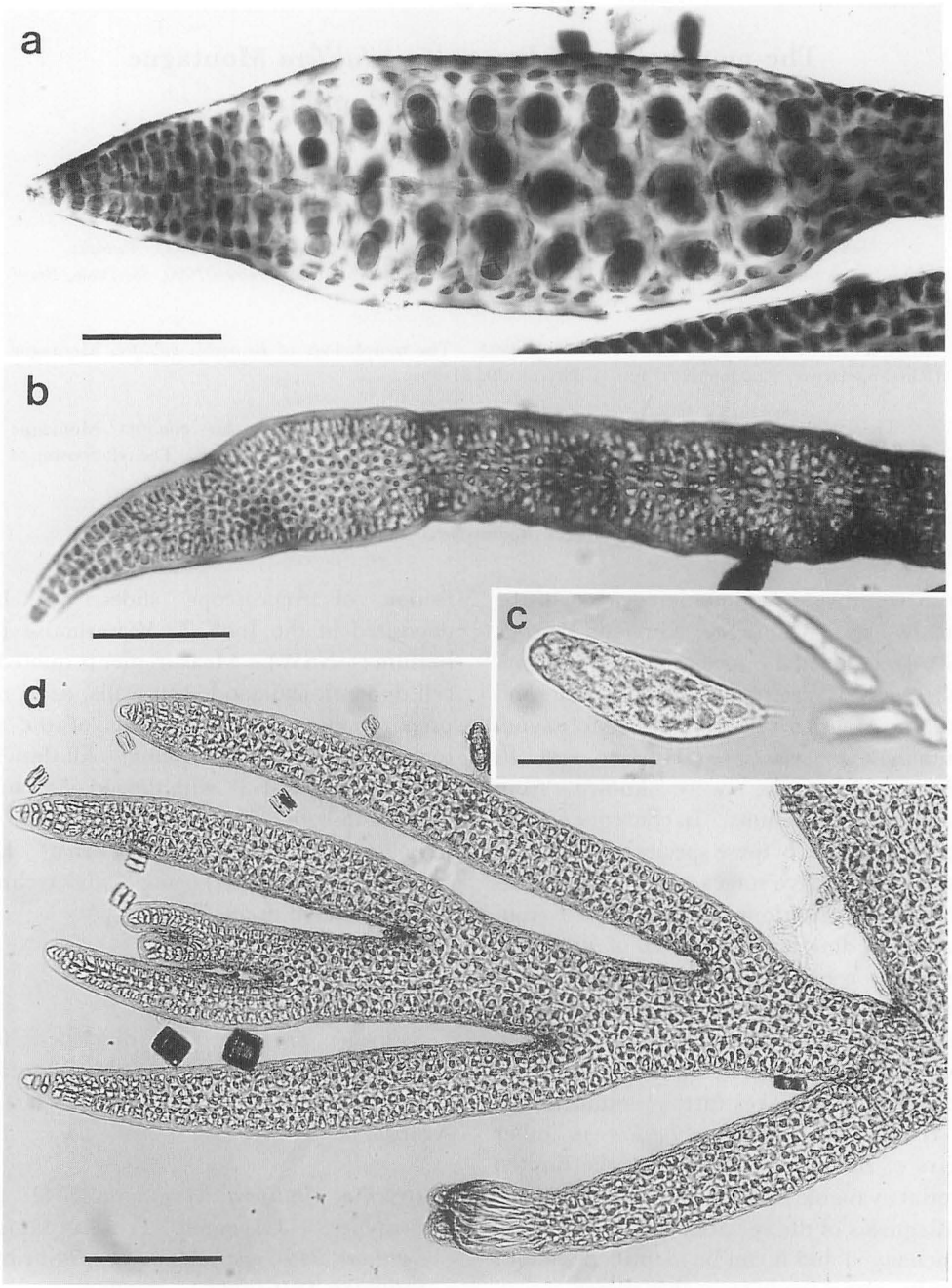


Fig. 1. *Paula*, SPF 54449 ⊕, ♂, ♀ respectively. a. Tetrasporangial stichidium, showing the five tetrasporangia around the axial cells. Scale: 100 μm. b. Spermatangial branch with apical portion fertile and lower part now devoid of spermatia. Scale: 100 μm. c. Gonimoblast filament exhibiting sympodial growth and with a terminal carposporangium. Scale: 50 μm. d. Determinate (lateral) branching system arising from an indeterminate branch. The hapteral branch (lower) has a rhizoidal apex. Other branches show the typical single celled apex, and young tetrasporangial stichidia are visible in the upper branches. Scale: 200 μm.

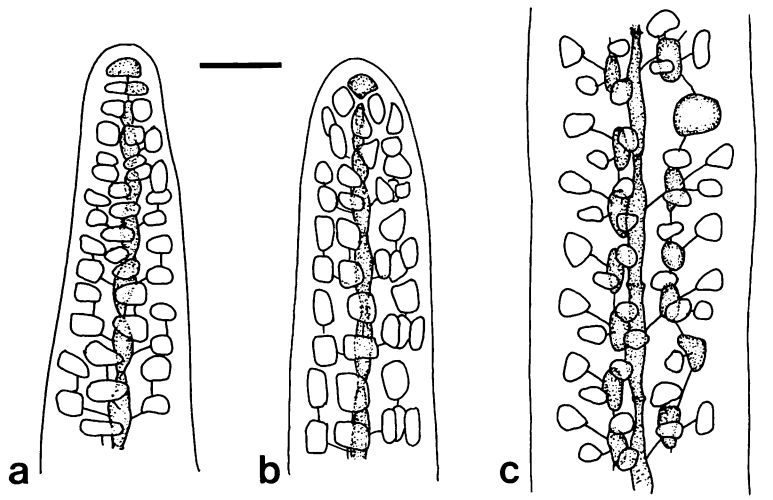


Fig. 2. *Paula*, SPF 54449. Scale: 100 μm. a. Vegetative apex; axial cells stippled. b. Hapteral apex. c. Cortical development; cells derived from two pericentral cells only shown. Most proximal pericentral cells give rise directly to four cortical cells, and distal cells give rise to 0–3 cortical cells.

tagne) Kützing 1847: 3.
*Amphibia pilulifera* (Montagne) Kuntze 1891: 881.

*Description* (Figs. 1-3)

*Thallus* scrambling with sub-erect branches or more or less prostrate, robust, clump or turf-forming, purple to brown; main axes indeterminate, 35-70 mm long bearing determinate lateral branches 2-3 mm long, with 1-2 (-3) orders of alternate branching (5-13 second order determinate branches); 2 tiers of pericentral cells per axial cell, with (6-) 7-8 pericentral cells per tier around the main axes and primary lateral branches; (4-) 5-6 pericentral cells per tier in fertile branches; corticate throughout (except distal portion of male reproductive branches polysiphonous); attached to the substratum by cladohaptera.

*Indeterminate axes* 120-600 μm in diameter, axial cells 80-400 μm long; cortex well developed, 2-3 orders of cortical cells; superficial cortical cells rectangular to ovoid 15-25 μm long, 8-12 μm wide; branches arising alternately at intervals of 5 or more axial cells; determinate branches arising laterally at intervals (2-) 4-6 axial cells. *Determinate branches* of 1-2 (-3) orders, branching at intervals of 2-5 (-10) axial cells; ultimate branches 25-45 axial cells long. *Cladohaptera* 8-10 axial cells long; branch borne from the first axial cell of primary lateral branches. Cladohaptera that do not become attached to the substratum have the appearance of short unbranched laterals of determinate growth. *Carpogonial branches* borne within 5-7 subapical axial cells of lateral branches; fertile region usually 1-3 consecutive axial cells long with 1 procarp per axial cell; axial cells below the fertile region have 5-7 pericentral cells per tier and procarpial axial cells 5 pericentral cells per axial cell; the supporting cell produces a sterile group of 3 cells prior to fertilization and the adjacent sterile pericentral cell produces a group of 3-5 cells; the carpogonial branch is 3 cells long. *Cystocarps* subapical, ovoid to globular, 500-600 μm long, 450-500 μm in diameter, with a 50-80 μm diameter ostiole; cystocarp walls have 8 longitudinal pericarp filaments with two 2-tiered pericarp pericentral cells per filament cell and 1-2 orders of cortical cells; carposporangia 88-100 μm long, 25-35 μm in diameter, 40-70 per cystocarp. *Spermatangial branches* 800-1500 μm long, 85-110 μm in diameter, formed from 3-12 subapical axial cells (350-400 μm) of ultimate lateral branches fertile, and older proximal sper-

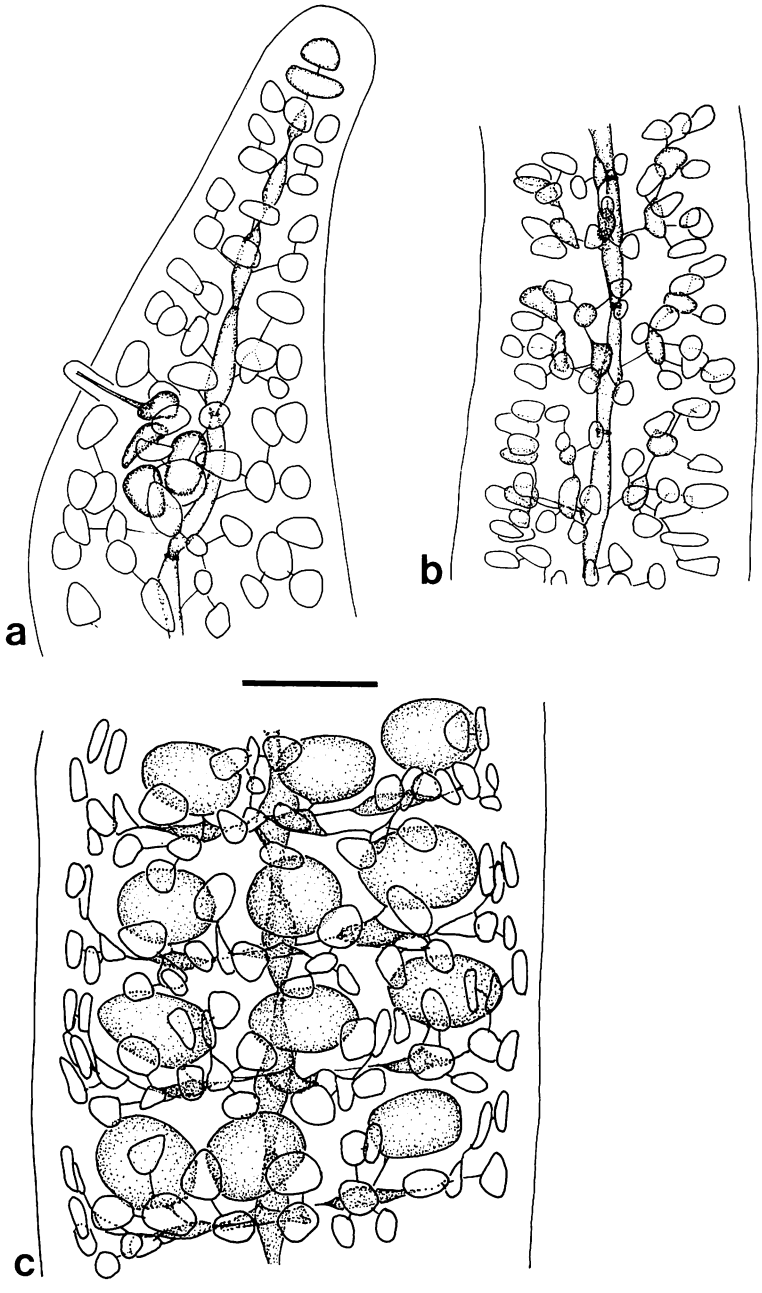


Fig. 3. *Paule*, SPF 54449 ♀, ♂, ⊕ respectively. Scale: 100 μm. a. Procarpial branch; axial cells and procarp stippled. b. Spermatangial branch; all cells derived from three pericentral cell rows only shown. c. Tetrasporangial stichidium; for four pericentral cell rows only.

matogenous superficial cells spent; axial cells below the fertile region have (4–) 5 pericentral cells per tier; spermatangial branches have 5 pericentral cells around the axial cell, giving rise to 2 tiers of pericentral cells; each pericentral cell produces 1 (-2) orders of cortical cells, the superficial cells are potentially spermatogenous. *Tetrasporangia* borne in subapical stichidia on ultimate lateral branches; stichidia 700-1200 μm and 7-10 axial

cells long, 195–250 μm in diameter; branches bearing stichidia have 6 pericentral cells per tier; stichidia have 5–6 pericentral cells per axial cell, each of which gives rise to a tetrasporangium and 2 cover cells, each cover cell divides once and subsequently forms 0–1 order of cortical cells; tetrasporangia 50–65 μm in diameter.

*Distribution and habitat*

Endemic to the northeast coast of South America: French Guiana, Surinam and Brazil; probably widespread in this region but as yet poorly collected. *Bostrychia pilulifera* grows epiphytically on mangroves in the upper eulittoral zone, in both the full sun and shade. Plants growing in full sun tend to be short and prostrate whereas shade plants are longer and erect, and in consequence fewer of the hapteral branches are attached to the substratum.

*Specimens examined*

SOUTH AMERICA: French Guiana: Cayenne, [1839–1843] *Leprieur 349 and Montagne* (syntype: MEL 672280, labelled '*Rhodomela floccosa? junior?*'). Surinam: [Nov. 1837–July 1838] *Splitgerber* 1316/1317 (syntype: MEL 672281); Surinam R., N of Paramaribo, 26. vii. 1958, *Vroman* (BISH). Brazil: Ilha de Maracá [N of Amazon R. delta, c.2°N 50°W] 21. x. 1988, *Paula* (SPF 54449 ♀, ♂, ⊕, 54065); Baia de Marajó, Mosqueiro, [c.1°S 48°W] 2. ii. 1988, *Ugadim* (SPF 51927, 52026, 52046).

*Etymology*

Montagne (1842) presumably named this species because of its "*globoso-subovatis*" cystocarps: from *pilula* (a globule) and *fera* (to bear), though this is typical of all species of *Bostrychia*.

## Discussion

The production of the hapteron is identical to that found in *Bostrychia radicans* (Montagne) Montagne and *B. moritziana* (Sonder ex Kützing) J. Agardh: a vegetative branch dedicated to the development of a terminal holdfast is produced from the first axial cell of the determinate lateral branch system (Fig. 1d). This branch is initiated in the direction of the substratum instead of more or less in the horizontal plane, as is typical of all other branching. Although this branch is directed towards the substratum it actually emerges between the second and fourth formed pericentral cell row because of the rotation of the formation of pericentral cells in lateral branches. The first formed pericentral cell row is in the upper abaxial position and the last formed is in the adaxial position. The branch arising from the first axial cell of determinate branches of *B. radicans, B. moritziana* and *B. tenella* (Lamouroux) J. Agardh is likewise in this position. Hapteral branches (Fig. 1d, 2b) can be distinguished from other branches by the cluster of extended pericentral cells associated with the apex.

In tetrasporangial plants of *Bostrychia pilulifera* (Fig. 1a, 3c) the pattern of cover cell production is the same as that in *B. radicans* and *B. moritziana*, with two cover cells produced to the outside of the stalk cell. Each of these two cover cells cuts off one cell anteriorally. In *B. pilulifera* this is followed by the production of a further layer of cortical cells. In other species of *Bostrychia* three cover cells are produced.

The morphology of the procarp (Fig. 3a), cystocarp, and carpospore (Fig. 1c) of *B. pilulifera* are the same as those of other species of *Bostrychia*.

Male plants possess fertile lateral branches which produce spermatia over some length of time. Spermatogenous cells of the subapical region (350–400 μm) are active in producing spermatia and for up to 1100 μm behind this is a region that had produced spermatia in the past but is now inactive (Fig. 1b, 3b). The superficial ex-spermatogenous (spent) cells provide no evidence of secondary activity. The same pattern is seen in *Bostrychia radicans* (see Fig. 10b in King and Puttock, 1989). No spent spermatogenous regions have been found in other species such as *B. tenuissima, B. pinnata* and *B. moritziana* (King and Puttock

1989; Fig. 8d, 9a, 13e) nor in the cultured plants of *B. tenella* (West and Calumpong 1988).

Cortical development of *Bostrychia pilulifera* differs in detail from that in other corticated species (Fig. 2c). The pericentral cells are formed in two tiers as is typical for the genus (King and Puttock 1989). The additional two or three layers of cortical cells cut off to the outside may also follow this same pattern. However, frequently the outermost layer of the cortex diverges from this pattern with the cells of the penultimate cortical layer producing four cortical cells directly (Fig. 2c; see also Fig. 4a in King and Puttock 1989). Unlike the cells of the outer cortical layer in other corticate species these cells do not form secondary pit connections with the cells of the same order from adjacent anterior and posterior cells.

**Conclusions:**

The availability of this additional material has provided confirmation of the details of the diagnosis for *Bostrychia pilulifera* in King and Puttock (1989) including the presence of cladohaptera (Post 1936). The pattern of development shown by *B. pilulifera* is the same as that in *B. radicans*, but *B. pilulifera* is readily distinguished by the cortication of the main axes and the well developed indeterminate axis (35-70 mm long c.f. 10-20 mm in *B. radicans*).

In addition, one of the underlying predictions of the cladistic analysis in King and Puttock (1989) was that the cortication has arisen on several occasions. The superficial cortical layer in *B. pilulifera* is developed in a different manner to that in other corticated species of *Bostrychia*, which is consistent with the notion that cortication has arisen on several occasions, and is not homologous at least between *B. pilulifera* and its species group (*B. radicans*) in the cladistic analysis, and the other groups.

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**R. J. King*·C. F. Puttock*·E.J. Paula**: 紅藻コケモドキ属の 1 種 *Bostrychia pilulifera* の形態**

紅藻フジマツモ科コケモドキ属の 1 種 *Bostrychia pilulifera* Montagne の栄養体の形態ならびに全ての生殖段階を，ブラジルで近年採集した標本について詳細に記載した。本種とコケモドキ属の他の種との関係についても論議した。
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