

# Morphological Study of Nine Taxa of *Bostrychia* (Rhodophyta) from Southwestern Japan, Hong Kong and Guam<sup>1</sup>

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**Abstract.**—The comparative morphology of nine taxa of the genus *Bostrychia* collected from Southwestern Japan, Hong Kong and Guam is presented. The number of pericentral cells of each central cell ranges from two to four among the taxa. The uppermost pericentral cell of taxa examined always contains two nuclei. The flagellar haptera of *Bostrychia tenuis* f. *simpliciuscula*, *B. hamana-tokidai*, *B. binderi*, *B. tenella* and *B. mixta* consist of ventral and side pericentral cells. *B. radicans*, *B. moritziana*, *B. kelanensis* and *Bostrychia* sp. have hapteronous branches transformed from the ordinary branches. In some taxa, new buds are formed at tips of hapteronous branches. In *B. radicans* and *B. moritziana* an erect branch and a hapteronous branch are successively initiated from the main axis. Each tetrasporangium of the taxa examined is accompanied by a tetrasporangium mother cell linked by pit-connections with both a central cell and the lowermost cover cell.

## Introduction

*Bostrychia* is a genus characteristic of vegetation in temperate seas and often of mangrove communities in tropical seas. The early taxonomists such as Kützing (1849) and J. Agardh (1863) classified the genus *Bostrychia* mainly on the number of pericentral cells in transverse direction and the mode of branching. Post (1936) revised the taxonomy of the genus *Bostrychia* and based it on the kind of haptera, the number of pericentral cells in longitudinal direction, the cortication of the thallus and the poly- or monosiphonous ultimate branchlets. Moreover, she described some new species (Post, 1939, 1941). The pericentral cell formation and the cortical cells were observed by Falkenberg (1901), the haptera formation by Falkenberg (1901) and Tokida (1938, 1939) and the tetrasporangial development by Falkenberg (1901).

This paper deals with some observations of the thallus structure, the haptera formation and the tetrasporangial development of nine taxa of the genus *Bostrychia* in comparison with some taxa of the Rhodomelaceae and the Delesseriaceae.

The material collected were preserved in 10% formalin solution. For cytological study, the materials were fixed with an aceto-alcohol (3:1) solution and stained with Wittman's aceto-iron-haematoxylin chloral hydrate solution.

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## KEY TO THE NINE TAXA OF BOSTRYCHIA

1. Flagellar haptera consisting of ventral and side pericentral cells.
  2. Non-corticated.
    3. Two whorls of pericentral cells to each central cell.
      4. Ultimate branchlets polysiphonous. . . . . *B. tenuis* f. *simpliciuscula*
      4. Ultimate branchlets always monosiphonous. . . . . *B. hamana-tokidai*
    3. Four whorls of pericentral cells to each central cell . . . . . *B. mixta*
  2. Corticated.
    5. Ultimate branchlets of the last order polysiphonous at the base, only apical segments monosiphonous. . . . . *B. binderi*
    5. Ultimate branchlets of the last order all monosiphonous. . . . . *B. tenella*
1. Hapteronous branch transformed from the ordinary branch.
  6. Three whorls of pericentral cells to each central cell.
    7. No bud formed at the tips of hapteronous branches. . . . . *B. kelanensis*
    7. New bud formed at the tips of hapteronous branches. . . . .  
 . . . . . *Bostrychia* sp.
  6. Two whorls of pericentral cells to each central cell.
    8. Ultimate branchlets polysiphonous. . . . . *B. radicans*
    8. Ultimate branchlets all monosiphonous. . . . . *B. moritziana*

## Species

*Bostrychia tenuis* Post f. *simpliciuscula* Post

Figs. 1, 2, 4-6

The frond is dark purplish brown, densely tufted, vaguely branched, ecorticate; the ultimate branchlets are polysiphonous.

The dome-shaped apical cell cuts off segments posteriorly by transverse divisions. The segment soon divides by longitudinal walls to produce 4-5 pericentral cells, which divide transversely as shown in Fig. 1. Two whorls of pericentral cells occur with each central cell; the lower pericentral cells ( $p_1$ ) thus formed retain pit-connections with the central cell (Fig. 2). The central cell and the lower pericentral cells contain one nucleus. However, the upper pericentral cells ( $p_2$ ) contain two nuclei as shown in Fig. 2.

The hapteron is the special flagellar outgrowth consisting of the ventral and side pericentral cells ( $p_1$ ,  $p_2$ ) produced from a segment; however, the dorsal pericentral cells do not take part in the hapteron formation. The ventral and side pericentral cells ( $p_1$ ,  $p_2$ ) produced from a segment elongate and then divide into several cells (Figs. 4 and 5). During development, the hapteron bends towards the substratum (Fig. 6).

The specimens were collected by S. Kumano on April 5, 1977, from a fall in the Arakawa River, Ishigaki Island, and by M. Shundo on May 26, 1978, from the Mariudo Fall in the Urauchi River, Iriomote Island, Okinawa Prefecture, Japan.

*Bostrychia hamana-tokidai* Post

Figs. 7-11

The frond is dark reddish brown, very small, tufted, ecorticate; the ultimate branches are always monosiphonous.

The apical cell of the thallus is large and conspicuous, cuts off a saucer-shaped segment by transverse division. These segments soon initiate the pericentral cells; 4-6 pericentral cells are cut off by longitudinal walls and then divide once transversely ( $p_1$ ,  $p_2$ ). The lower pericentral cells ( $p_1$ ) retain pit-connections with a central cell (ax) as shown in Fig. 7. The branch is cut off directly from the subapical cell before pericentral cell formation. The segments of the ultimate branchlets do not initiate the pericentral cells; the ultimate branchlets are always monosiphonous (Fig. 7).

The hapteron is affected by the outgrowth of pericentral cells produced from two or three segments. The pericentral cells, produced from the segment from which a branch often arise, are involved in the hapteron formation. The ventral and side pericentral cells ( $p_1$ ,  $p_2$ ) produced from a segment elongate and then divide into several cells as shown in Fig. 8. During hapteron development, the pericentral cells produced from the overlying segment and the underlying segment also take part in hapteron formation (Figs. 8 and 9).

The terminal portions of some branches are converted into tetrasporangial stichidia with tetrahedrally-divided tetrasporangia in each tier (Fig. 11); the intercalary stichidia are also observed (Fig. 10). Each tetrasporangium (t) is accompanied by two sets of two cover cells ( $c_1$ ,  $c_2$ ) and the tetrasporangium mother cell (m), which is linked by primary pit-connections with a central cell (ax) and the lower cover cell ( $c_1$ ) as shown in Figs. 10 and 11.

The specimens were collected by M. Shundo on May 24, 1978, from the Hinai River, Iriomote Island, Okinawa Prefecture, Japan.

*Bostrychia mixta* Hooker et Harvey

Figs. 3, 12-15

The frond is creeping, dichotomously branched, ecorticate; the ultimate branches are always polysiphonous.

A large apical cell cuts off discoid segments posteriorly. These segments soon divide by longitudinal walls to produce 6 pericentral cells. The branches are cut off directly from the subapical cells before pericentral formation; each pericentral cell divides transversely up to four cells ( $p_1$ ,  $p_2$ ,  $p_3$ ,  $p_4$ ); four whorls of pericentral cells occur with each central cell (ax). Only the lowermost pericentral cells ( $p_1$ ) retain pit-connections with a central cell (ax) as shown in Fig. 3. The central cell (ax) and the lower three pericentral cells ( $p_1$ ,  $p_2$ ,  $p_3$ ) contain one nucleus; however, the uppermost pericentral cells contain two nuclei as shown in Fig. 12.

The hapteron is the special outgrowth consisting of the pericentral cells produced from two segments. Usually the ventral pericentral cells produced from a segment are involved in hapteron formation. The lower two pericentral cells ( $p_1$ ,  $p_2$ ) are produced

from a segment, and then the uppermost pericentral cells ( $p_4$ ), produced from the underlying segment, elongate and then divide into two cells. During hapteron development, the upper two pericentral cells ( $p_3$ ,  $p_4$ ) produced from a segment also take part in hapteron formation (Figs. 13 and 14).

The tetrasporangial stichidia are incurved, lanceolate, and produced from the distal parts of the branches. The tetrasporangia are formed in an indeterminate succession so that the oldest one is nearest the base. The fertile pericentral cell cuts off a cover cell initial ( $c$ ), which divides into two or three cover cells ( $c_1$ ,  $c_2$ ,  $c_3$ ). After cover cell formation, the tetrasporangium ( $t$ ) is initiated on the apical side from the long tetrasporangium mother cell ( $m$ ), which is linked by pit-connections with a central cell ( $ax$ ) and the lowermost cover cell ( $c_1$ ). The sterile pericentral cells occur on the dorsal side of the tetrasporangial stichidium and divide into four pericentral cells as in the vegetative portion, so that the stichidium is often asymmetric and incurved as shown in Fig. 15.

The specimens were found on rocks in a mangrove community at Tsim Bei Tsui Point, Yuen Long District, New Territories, Hong Kong by S. Kumano on September 23, 1977.

*Bostrychia binderi* Harvey

Figs. 16–23

The frond is dull purplish, matted, tripinnate, parenchymously corticate; the ultimate branchlets are rather short, spinuliform and polysiphonous; only the tip is monosiphonous.

The apical cell on the thallus is dome-shaped and cuts off segments posteriorly by transverse divisions. These segments divide by longitudinal walls to produce several pericentral cells, which divide transversely into two pericentral cells ( $p_1$ ,  $p_2$ ). At first the lower pericentral cell ( $p_1$ ) cuts off a cortical cell initial ( $c'$ ) by an oblique division and then the upper pericentral cell ( $p_2$ ) divides transversely to produce a cortical cell initial ( $c'$ ) as shown in Fig. 16. These cortical cell initials divide to form the cortical layer of cells (Figs. 17 and 18).

The branches are cut off directly from the subapical cells; the axial segment divides to produce a pericentral cell ( $p_1$ ) on one side and a branch initial ( $bi$ ) on the other side. The branch initial ( $bi$ ) cuts off a branch segment posteriorly, the axial segment produces one more underlying pericentral cell ( $p$ ), which can divide into two cells, on the same side where the branch initial ( $bi$ ) was formed as shown in Fig. 19. The pericentral cells on the other side divide into two cells ( $p_1$ ,  $p_2$ ). The basal segment ( $b$ ) of the branch divides to produce pericentral cells. The ultimate branchlets thus formed are polysiphonous, but remain monosiphonous at the tips of the branchlets (Fig. 20).

The hapteron is a special flagellar outgrowth consisting of the pericentral cells produced from two segments. The ventral and side pericentral cells ( $p_1$ ,  $p_2$ ) produced from a segment, elongate and then divide into several cells. Some of the pericentral cells produced from the underlying segment also take part in hapteron formation as shown in Figs. 21 and 22.

The tetrasporangial stichidia are formed from the distal parts of the branchlets. The apical cell of the tetrasporangial stichidium cuts off segments by transverse divisions in the same manner as the vegetative thallus. These segments, thus formed, divide by longitudinal walls to produce the pericentral cells, each of which divides longitudinally to produce a cover cell initial (c) and a tetrasporangium mother cell (m). After the cover cells ( $c_1$ ,  $c_2$ ,  $c_3$ ) have been initiated, the tetrasporangium (t) is cut off by a transverse wall from the tetrasporangium mother cell (m); the remaining portion of the mother cell is referred to as a stalk cell. In each segment 4–5 tetrasporangia are formed. Each tetrasporangium (t) is accompanied by two or three cover cells ( $c_1$ ,  $c_2$ ,  $c_3$ ) and a tetrasporangium mother cell (m) linked by pit-connections with a central cell (ax) and the lowermost cover cell ( $c_1$ ) as shown in Fig. 23.

The specimens were found on rocks near the Okura Hotel at Gognga Beach, Tumon Bay, Guam by S. Kumano on March 31, 1978.

*Bostrychia tenella* (Vahl) J. Agardh

Figs. 24–32

The frond is dull reddish purple, matted, densely tufted, repeatedly pinnate, corticate; the ultimate branchlets are monosiphonous.

A large apical cell of the thallus cuts off a discoid segment posteriorly. The segment divides by longitudinal walls to produce 6–8 pericentral cells, which divide once transversely into two pericentral cells ( $p_1$ ,  $p_2$ ) as shown in Fig. 24. The lower pericentral cells ( $p_1$ ) cut off a cortical cell initial ( $c'$ ) by concave division, and the upper pericentral cells ( $p_2$ ) also cut off cortical cell initials ( $c'$ ) in the same manner (Fig. 25). As the cortical cell initially produced from the upper pericentral cell ( $p_2$ ) divides into two ( $c'$ ,  $c'$ ), the lower pericentral cell ( $p_1$ ) produces one more cortical cell ( $c'$ ) as shown in Fig. 26. The cortical layer of cells is thus formed.

The branch is formed from the subapical cell; the axial segment divides to produce a pericentral cell ( $p_1$ ) on one side and a branch initial (bi) on the other side. As the pericentral cell on one side divides into two ( $p_1$ ,  $p_2$ ), the branch initial (bi) on the other side also cuts off the branch segment (b) posteriorly. One more pericentral cell (p) is produced from the axial segment on the same side where the branch is initiated. The basal segment (b) of the branch divides to produce pericentral cells (Figs. 27–29). The ultimate branchlets are monosiphonous and produced in the simpler manner; the central cells of the branchlets are accompanied by one whorl of pericentral cells and each segment of the ultimate branchlets does not produce any pericentral cell (Fig. 30).

The hapteron is a flagellar outgrowth of the pericentral cells produced from two segments. The ventral and side pericentral cells ( $p_1$ ,  $p_2$ ) produced from a segment are involved in hapteron formation, that is, they elongate and divide into several cells. Some of the pericentral cells produced from the underlying segment also take part in hapteron formation as shown in Figs. 31 and 32.

The specimens were found on the rocky wall in Marbo Cave, Campanaya Point, Guam by S. Kumano on March 31, 1978.

*Bostrychia kelanensis* Grunow

Figs. 33-37

The frond is dark reddish brown, small, threadlike, irregularly branched, ecorticate; the branches are polysiphonous.

The apical cell of the thallus is large and cuts off a discoid segment which divides by longitudinal walls to produce several pericentral cells. These pericentral cells divide transversely into two pericentral cells ( $p_1$ ,  $p_2$ ). The upper pericentral cells ( $p_2$ ) divide once more, so that three whorls ( $p_1$ ,  $p_2$ ,  $p_3$ ) of the pericentral cells occur with each central cell (ax). The lowermost pericentral cells ( $p_1$ ) retain pit-connections with a central cell (ax). The central cell (ax) and the lower pericentral cells ( $p_1$ ,  $p_2$ ) contains one nucleus. However, the uppermost cell ( $p_3$ ) contains two nuclei as shown in Fig. 33.

The hapteron is a transformed branch produced at the ordinary position of the branch. At the tip of the transformed branch, the apical cell of the branch stops to produce the segments posteriorly and elongates downwards as shown in Fig. 34. At the same time, the pericentral cells (p) produced from the apical cell and the central cell (ax) elongate along the axis before they divide into three as in the normal pattern (Fig. 35). The clusters of threads consisting of elongated central cells (ax) and pericentral cells (p) form the hapteron, which bends over towards the substratum (Fig. 36).

The tetrasporangial stichidia are fusiform and develop at the tips of the branches. The apical cell of the tetrasporangial stichidium cuts off segments by transverse divisions in the same manner as the vegetative thallus. These segments divide by transverse walls to produce pericentral cells, each of which divides by a longitudinal wall to form a cover cell initial (c) and a tetrasporangium mother cell (m). After the cover cell initial (c) has been formed and divides into two cover cells ( $c_1$ ,  $c_2$ ), a tetrasporangium (t) is cut off transversely from the mother cell (m); the remaining portion of the mother cell is referred to as a stalk cell. Each tetrasporangium (t) is accompanied by a tetrasporangium mother cell (m) linked by pit-connections with a central cell (ax) and the lower ones ( $c_1$ ) of two sets of three cover cells ( $c_1$ ,  $c_2$ ,  $c_3$ ) as shown in Fig. 37.

The specimens were found on the substratum in the Ylig River by S. Kumano on April 3, 1978 and on rocks under the Old Spanish Bridge in the Taleyfac River, Guam by S. Kumano on April 2, 1978.

*Bostrychia* sp.

Figs. 38-44

The frond is dark brown, very small, somewhat erect, attaching by large haptera, ecorticate and polysiphonous.

The dome-shaped apical cell of the thallus cuts off segments posteriorly. These segments soon divide by longitudinal walls to produce several pericentral cells. The pericentral cell divides into two pericentral cells; the upper one divides once more, so



that three whorls of pericentral cells ( $p_1$ ,  $p_2$ ,  $p_3$ ) occur with each central cell (ax). The lowermost pericentral cell ( $p_1$ ) retains a pit-connection with the central cell (ax). The uppermost pericentral cells ( $p_3$ ) contain two nuclei. However, the central cell (ax) and the other pericentral cells ( $p_1$ ,  $p_2$ ) contain only one nucleus as shown in Figs. 38 and 39.

The hapteron is transformed from the ordinary branch. The apical cell of the transformed branch does not produce the discoid segment posteriorly but elongates downwards. The pericentral cells (p) produced from the apical cell and the central cell (ax) elongate along the axis at the same time; the clusters of threads, consisting of the elongated pericentral cell (p) and the central cell (ax), bend over towards the substratum. The hapteron functions as a stolon from which a new thallus is developed. The new bud is often initiated from the central cell (ax) on the third or fourth segment behind the apex of the hapteron at the stage when the hapteron begins to develop. The central cell (ax) cuts off the branch initial which divides to produce a new bud. The basal segment (b) of the new bud produces one or two pericentral cells (Figs. 40-42).

The tetrasporangial stichidia are formed at the tips of the branches. An apical cell of the tetrasporangial stichidium cuts off segments by transverse divisions in the same manner as the vegetative thallus. The segment divides by longitudinal walls to produce pericentral cells. Each pericentral cell divides once more by a longitudinal wall to produce a cover cell initial (c) and a tetrasporangium mother cell (m). The cover cell initial (c) divides into three cover cells ( $c_1$ ,  $c_2$ ,  $c_3$ ), then a tetrasporangium (t) is cut off transversely from a tetrasporangium mother cell (m). Each tetrasporangium (t) is accompanied by a tetrasporangium mother cell (m) linked by pit-connections with a central cell (ax) and the lowermost ( $c_1$ ) of two sets of three cover cells ( $c_1$ ,  $c_2$ ,  $c_3$ ) as shown in Figs. 43 and 44.

The specimens were found in mangrove communities in estuaries of the Nozoko River by S. Kumano on April 5, 1977, the Nakura River by M. Shundo on May 23, 1978 on Ishigaki Island, the Hinai River by M. Shundo on May 24, 1978 on Iriomote Island, Okinawa Prefecture, Japan and the Ajayan River, Guam by S. Kumano on April 3, 1978.

### *Bostrychia radicans* Montagne

Figs. 45-50

The frond is dull purplish, erect above, creeping below, attaching by haptera, pinnately branched, ecorticate and polysiphonous.

The apical cell of the thallus is large and cuts off discoid segments, which divide by longitudinal walls to produce several pericentral cells. These pericentral cells divide transversely into two pericentral cells ( $p_1$ ,  $p_2$ ). The upper pericentral cells ( $p_2$ ) contain two nuclei, but the central cell (ax) and the lower pericentral cells ( $p_1$ ) contain only one nucleus as shown in Fig. 45.

At the tips of the thallus, the erect branch (B) and the hapteronous branch (H)

are successively initiated from the main axis (M) as shown in Fig. 46. The erect branch (B) is initiated from the subapical cell of the main axis, that is, the axial segment, namely the central cell, cuts off the first initial to be developed into the erect branch (B). The basal segment (b) of the erect branch cuts off the branch initial which is transformed into the hapteron. The main axis (M) and the two branches (B, H) thus formed have different functions, respectively; the main axis (M) functions as a stolon, the erect branch (B) grows upwards and the hapteronous branch (H) bends over towards the substratum as shown in Figs. 46 and 47. At the tip of the hapteronous branch, the apical cell (ax) terminates to produce discoid segments posteriorly and elongates downwards. The pericentral cells (p) produced from the apical cell and the central cells (ax) also elongate along the axis. The clusters of these threads consisting of the central cells (ax) and the pericentral cells (p) bend over towards the substratum (Figs. 48 and 49).

The tetrasporangial stichidia develop below the tips of the erect branches. The apical cell of the tetrasporangial stichidium cuts off segments by transverse divisions. These segments divide by longitudinal divisions to produce pericentral cells, each of which divides by a longitudinal wall to form a cover cell initial (c) and a tetrasporangium mother cell (m). After cover cells ( $c_1$ ,  $c_2$ ) have been initiated, a tetrasporangium (t) is cut off transversely from the tetrasporangium mother cell (m). Each tetrasporangium (t) is accompanied by a tetrasporangium mother cell (m) linked by pit-connections with a central cell (ax) and the lower ones ( $c_1$ ) of two sets of two cover cells ( $c_1$ ,  $c_2$ ) as shown in Fig. 50.

The specimens were collected from mangrove communities in estuaries of the Nozoko River by S. Kumano on April 5, 1977, the Nakura River by M. Shundo on May 23, 1978 on Ishigaki Island, and the Urauchi River by M. Shundo on May 26, 1978 on Iriomote Island, Okinawa Prefecture, Japan.

*Bostrychia moritziana* (Sonder) J. Agardh

Figs. 51–59

The frond is dull reddish purple, rather erect, repeatedly pinnate, ecorticate; the ultimate branchlets are monosiphonous only at the tip.

The apical cell of the thallus is large, conspicuous and cuts off a saucer-shaped segment by transverse division. The segment divides by longitudinal walls to produce 7–8 pericentral cells, which divide once transversely into two pericentral cells ( $p_1$ ,  $p_2$ ). The lower pericentral cells ( $p_1$ ) thus formed retain pit-connections with the central cells (ax) as shown in Fig. 51. The branch is cut off directly from the subapical cell before pericentral cell formation. The branch initial (bi) is cut off from the central cell (ax) by an oblique concave wall. The ultimate branchlets are monosiphonous but polysiphonous at the base (Figs. 51 and 52).

At the tip of the thallus, the lateral branch (B) and the hapteronous branch (H) are successively initiated from the main axis (M) as shown in Fig. 53. The lateral branch (B) is initiated from the subapical cell and then the basal segment (b) of the



lateral branch (B) cuts off the second branch initial (h) by an oblique concave wall which is then transformed into a hapteronous branch (Figs. 54 and 55). At the tip of the hapteronous branch, the apical cell stops to produce discoid segments posteriorly; the pericentral cells (p) produced from the apical cell and the central cell (ax) elongate along the axis as shown in Fig. 56. The hapteron thus formed bends over towards the substratum. The bud of the new thallus is sometimes produced at the tip of the hapteron; a new bud is initiated from the central cell (ax) at about the third segment behind the apex of the hapteron. The central cell (ax) cuts off the branch initial to produce a new thallus (Fig. 57).

An apical cell cuts off segments transversely to form the tetrasporangial stichidia at the tips of the branchlets. These segments divide by longitudinal divisions to produce pericentral cells, each of which divides by a longitudinal wall to form a cover cell initial (c) and tetrasporangium mother cell (m). The cover cell initial divides into two cover cells ( $c_1$ ,  $c_2$ ), then a tetrasporangium (t) is cut off transversely from the tetrasporangium mother cell (m). Each tetrasporangium (t) is accompanied by a tetrasporangium mother cell (m) linked by pit-connections with a central cell (ax) and the lower ones ( $c_1$ ) of two sets of two cover cells ( $c_1$ ,  $c_2$ ) as shown in Figs. 58 and 59.

The specimens were found in the Hinai River, Iriomote Island, Okinawa Prefecture, Japan by M. Shundo on May 24, 1978.

### Discussion

*Thallus structure.* The transverse divisions of the pericentral cells are encountered in the tribe Rhodomeleae and the Bostrychieae of the family Rhodomelaceae. Kylin (1914) reported that in *Rhodomela virgata* of the Rhodomeleae each pericentral cell divides transversely, the uppermost pericentral cells retain the pit-connections with the central cell, while the lowest cells are linked by secondary pit-connections with the pericentral cells produced from the underlying segment. The pericentral cells cut off cortical cells, each of which again divides transversely.

*Bostrychia* of the Bostrychieae is also characterized by the fact that the pericentral cells divide transversely into two (e.g., *B. radicans*, *B. moritziana*), three (e.g., *B. kelanensis*) and four (e.g., *B. mixta*). Contrary to *Rhodomela*, all taxa of *Bostrychia* examined in the present paper show the lowermost pericentral cells retaining pit-connections with a central cell as already reported in *B. vaga* by Falkenberg (1901).

The cells of the less differentiated taxa in the Rhodophyta (the Bangiales and the Nemalionales) are always uninucleate and this character is also present in many taxa in the Cryptonemiales and the Gigartinales. In other instances, the older cells are multinucleate (the Gelidiales, the Rhodomenciales and many taxa in the Ceramiales), while in *Griffithsia* and *Bornetia* this is even true of the apical cells. As mentioned before, almost all cells are uninucleate at the tips of the thallus. However, the uppermost pericentral cells contain two nuclei in all taxa of *Bostrychia* examined in the present paper except in *B. tenella* and *B. binderi* where cortical cells are produced.

The lack of sufficient knowledge requires further comparative studies within the taxa of the Rhodomeleae.

*Hapteron formation.* Silva and Cleary (1954) stated that the thallus of *Platysiphonia parva* of the Sarcomenieae in the Delesseriaceae attaches to the substratum by an intricate system of rhizoids that arise as outgrowth of the various cells in the lower part of the frond, where the flanking cells were not formed by the lower two or three segments. Secondary attachment is affected by an outgrowth of a flanking cell. The rhizoid cleaves into several cells connected by conspicuous primary pit-connections. Hollenberg (1963) observed that in *Malaconema minimum* the thallus attaches by much branched multicellular rhizoids arising singly, usually from the segments from which the exclusively endogenous erect branches arise. These rhizoids are not cut off by a cross-wall from the pericentral cell bearing them.

Rosenvinge (1923–24) reported that in *Polysiphonia nigrescens* and *P. brodiaei* of the Polysiphonieae in the Rhodomelaceae the tips of the thallus crept over the substratum, to which they were firmly anchored by thick-walled, often richly lobed, unicellular rhizoid arising from a pericentral cell. *P. violacea* lacked this system of creeping threads and was merely attached by rhizoid arising from the lower cells of the erect axes.

The hapteron formation in *Bostrychia* of the Bostrychieae in the Rhodomelaceae was observed by some authors such as Falkenberg (1901) in *B. radicans* and *B. hookeri*, Tokida (1938) in *B. mixta*, and Tokida (1939) in *B. tenuis* f. *simpliciuscula*, *B. binderi* and *B. moritziana*. As already mentioned by many authors, the flagellar and branch hapteron are observed in nine taxa of *Bostrychia* in the present paper. The flagellar hapteron is formed by the pericentral cells, while the branch hapteron consists of the pericentral cells produced from the central cells and the central cells themselves.

*Tetrasporangium formation.* In *Platysiphonia parva* (Silva and Cleary, 1954) and *Malaconema minimum* (Hollenberg, 1963) of the Sarcomenieae in the Delesseriaceae, the tetrasporangia were reported to be produced usually in the ultimate branches of the thallus. Each lateral pericentral cell cuts off two flanking cells and then two tetrasporangia are formed in each segment. Two cover cells, first an abaxial cover cell and then an adaxial cover cell, are cut off after the tetrasporangium formation. In *Malaconema minimum* (Hollenberg, 1963) and *Platysiphonia miniata* (Weber van Bosse, 1896), the flanking cells were reported to divide by an arcuate transverse wall into a smaller anterior cell and a larger posterior cell. Silva and Cleary (1954) reported that during the tetrasporangial development in *Platysiphonia clevelandii* each flanking cell became markedly arcuate and divided transversely to form a marginal cell and a submarginal cell that comprised two cortical lobes, abaxial and adaxial. In *Lembergia allanii* near the Salcomenieae in the Delesseriaceae, Saenger et al. (1971) observed that the tetrasporangia were formed in two longitudinal rows after the flanking cells were cut off but before the cover cells were produced.

As mentioned above in the Delesseriaceae, the tetrasporangium mother cell first cuts off the tetrasporangium and then two cover cells; however, in the Rhodomelaceae this sequence is reversed.

In *Polysiphonia* of the Polysiphonieae in the Rhodomelaceae, the fertile pericentral cell first cuts off a daughter cell at its outer surface. In *P. nigrescens* (Kylin, 1923), the daughter cell was observed to cut off two cover cells at the upper surface; in *P. violacea* (Rosenvinge, 1923–24) and *Polysiphonia* sp. (Smith, 1938) the daughter cell was observed to cut off two larger cover cells and a small peripheral cell. In either case the fertile pericentral cell then divides transversely to produce a tetrasporangium. The lower daughter cell is a stalk cell and the upper is a tetrasporangium. The stalk cell is linked by primary pit-connections with a central cell and each cover cell or with each cover cell and a peripheral cell.

In *Rhodomela virgata* (Kylin, 1914) and *Odonthalia dentata* (Kylin, 1934) of the Rhodomeleae in the Rhodomelaceae, the fertile branches were reported to arise in tufts on the flanks, and in the former on the tips of the larger branches. The tetrasporangia originate from the two laterals of the six pericentral cells so that they form two longitudinal rows. The fertile pericentral cell cuts off a daughter cell, and then the daughter cell cuts off a large cover cell and a small peripheral cell. After cover cell formation, the tetrasporangium mother cell divides transversely to produce a tetrasporangium. The mother cell, referred as a stalk cell, is linked by primary pit-connections with a central cell, a cover cell and a peripheral cell, respectively.

In *Bostrychia* of the Bostrychieae in the Rhodomelaceae, the tetrasporangial stichidia are produced in the ultimate branches in which all the pericentral cells of a segment commonly become fertile. In certain species (*B. mixta*), those on the dorsal side remain sterile. In *B. hookeri* (Falkenberg, 1901) and seven taxa reported in the present paper, the fertile pericentral cell cuts off a cover cell, which divides into two or three cover cells. After cover cell formation, the tetrasporangium is initiated on the apical side from the tetrasporangium mother cell linked by pit-connections with a central cell and only the lowermost cover cell.

Silva and Cleary (1954) observed that the lateral pericentral cells function as the initials of the flanking cells in *Platysiphonia parva* of the Delesseriaceae. It is very interesting that even in some taxa, such as *Malaconema minimum* of the Delesseriaceae in which the vegetative thallus lacks the flanking cells, the typical delesseriaceous flanking cells are reported to form in the reproductive organs (Hollenberg, 1963). Silva and Cleary (1954) state that in taxa of the *Sarcomenia* group, the real cover cells are always formed after the tetrasporangium has been initiated, so that some protection is provided for the tetrasporangium by the transverse pericentral cells and the flanking cells, in addition to the cover cells.

Womersley and Shepley (1959) stated that the flanking cells of the stichidia in the *Sarcomenia* group should be interpreted as cover cells comparable to those of the Rhodomelaceae; however, Papenfuss (1961) stated that the flanking cells were not homologous to the cover cells of the Rhodomelaceae but to those of the vegetative thallus. I do not support the above mentioned two opinions, because the flanking cells

and the cover cells are different and independent from each other. Each flanking cell is linked by pit-connections with a tetrasporangium mother cell in the same manner as those of the vegetative thallus. The flanking cells of the Delesseriaceae are homologous to the cells such as two large cover cells and a small peripheral cell in *Polysiphonia violacea* and *Polysiphonia* sp., a cover cell and a peripheral cell in *Rhodomela virgata* and *Odonthalia dentata* of the Rhodomelaceae, which lack flanking cells. On the other hand, only the lowermost cover cell is linked by a pit-connection with a mother cell in all taxa of *Bostrychia* examined in the present studies. These cover cells were not homologous to the flanking cells of the Delesseriaceae. Further comparative studies with taxa of the Delesseriaceae and the Rhodomelaceae are required.

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### Explanation of Plates I to VII

#### Figs. 1, 2, 4-6. *Bostrychia tenuis* Post f. *simpliciuscula* Post

Fig. 1. Tip of thallus. A dome-shaped apical cell, discoid segments, a central cell and pericentral cells are shown. Fig. 2. Terminal portion of thallus. Two whorls of pericentral cells with each central cell are shown. Figs. 4-6. Flagellar hapteron formation. ax: central cell, p<sub>1</sub>, p<sub>2</sub>, p<sub>3</sub>, p<sub>4</sub>: pericentral cells.

Fig. 3. *Bostrychia mixta* Hooker et Harvey. Terminal portion of thallus. Four whorls of pericentral cells with each central cell are shown. ax: central cell, p<sub>1</sub>, p<sub>2</sub>, p<sub>3</sub>, p<sub>4</sub>: pericentral cells.

#### Figs. 7-11. *Bostrychia hamana-tokidai* Post

Fig. 7. Tip of ultimate branchlet. Two whorls of pericentral cells and monosiphonous condition are shown. Figs. 8 and 9. Flagellar hapteron formation. Fig. 10. Intercalary tetrasporangial stichidium. Fig. 11. Terminal tetrasporangial stichidium. Each tetrasporangium is accompanied by two sets of two cover cells and mother cell. ax: central cell, p<sub>1</sub>, p<sub>2</sub>, p<sub>3</sub>: pericentral cells, t: tetrasporangium, m: tetrasporangium mother cell, c: cover cell.

#### Figs. 12-15. *Bostrychia mixta* Hooker et Harvey

Fig. 12. Terminal portion of thallus. Four whorls of pericentral cells are shown. Figs. 13 and 14. Flagellar hapteron formation. Fig. 15. Terminal tetrasporangial stichidium. Sterile pericentral cells on dorsal side are observed. Each tetrasporangium is accompanied by two or three cover cells and a mother cell. ax: central cell, p<sub>1</sub>, p<sub>2</sub>, p<sub>3</sub>, p<sub>4</sub>: pericentral cells, t: tetrasporangium, m: tetrasporangium mother cell, c: cover cell.

#### Figs. 16-23. *Bostrychia binderi* Harvey

Fig. 16. Tip of thallus. A dome-shaped apical cell, pericentral cell and cortical cell formation are shown. Figs. 17 and 18. Terminal portion of thallus. Cortical cell formation is shown. Fig. 19. Branch formation. Fig. 20. Ultimate branchlets are polysiphonous but remain monosiphonous at tip. Figs. 21 and 22. Flagellar hapteron formation. Fig. 23. Terminal tetrasporangial stichidium. Each tetrasporangium is accompanied by two or three cover cells and a mother cell. ax: central cell, p<sub>1</sub>, p<sub>2</sub>: pericentral cells, c': cortical cell, bi: branch initial, b: basal segment of branch, t: tetrasporangium, m: tetrasporangium mother cell, c: cover cell.

Figs. 24–32. *Bostrychia tenella* (Vahl) J. Agardh

Figs. 24. Tip of thallus. A dome-shaped apical cell, central cells and two whorls of pericentral cells are shown. Figs. 25 and 26. Cortical cell formation. Figs. 27–29. Branch formation. Fig. 30. Monosiphonous ultimate branchlet. Figs. 31 and 32. Flagellar hapteron formation. ax: central cell, p<sub>1</sub>, p<sub>2</sub>: pericentral cells, c': cortical cells, bi: branch initial, b: basal segment of branch.

Figs. 33–37. *Bostrychia kelanensis* Grunow

Figs. 33. Tip of thallus. Three whorls of pericentral cells with each central cell are shown. Figs. 34–36. Hapteronous branch formation. Fig. 37. Terminal tetrasporangial stichidium. Each tetrasporangium is accompanied by two sets of three cover cells and a mother cell. ax: central cell, p<sub>1</sub>, p<sub>2</sub>, p<sub>3</sub>: pericentral cells, t: tetrasporangium, m: tetrasporangium mother cell, c: cover cell.

Figs. 38–44. *Bostrychia* sp.

Figs. 38 and 39. Terminal portion of thallus. Three whorls of pericentral cells with each central cell are shown. Figs. 40–42. Hapteronous branch and new thallus formation. Figs. 43 and 44. Terminal tetrasporangial stichidium. Each tetrasporangium is accompanied by two sets of three cover cells and a tetrasporangium mother cell. ax: central cells, p<sub>1</sub>, p<sub>2</sub>, p<sub>3</sub>: pericentral cells, b: basal segment of new thallus, t: tetrasporangium, m: tetrasporangium mother cell, c: over cell.

Figs. 45–50. *Bostrychia radicans* Montagne

Fig. 45. Tip of thallus. Two whorls of pericentral cells with each central cell are shown. Figs. 46 and 47. Hapteronous branch formation. Tip of thallus; an erect branch and a hapteronous branch are successively initiated from main axis. Figs. 48 and 49. Tip of hapteronous branch. Fig. 50. Terminal tetrasporangial stichidium. Each tetrasporangium is accompanied by two sets of two cover cells and a mother cell. ax: central cell, p: pericentral cell, b: basal segment of erect branch, h: basal segment of hapteronous branch, M: main branch, B: erect branch, H: hapteronous branch, t: tetrasporangium, m: tetrasporangium mother cell, c: cover cell.

Figs. 51–59. *Bostrychia moritziana* (Sonder) J. Agardh

Figs. 51 and 52. Tip of monosiphonous ultimate branchlets, but polysiphonous at base. Figs. 53–55. Hapteronous branch formation. A lateral branch and a hapteronous branch are successively initiated from main axis. Figs. 56 and 57. Tip of hapteronous branch and a new thallus formation. Figs. 58 and 59. Terminal tetrasporangial stichidia. Each tetrasporangium is accompanied by two sets of two cover cells and a mother cell. ax: central cell, p: pericentral cell, h: basal segment of hapteronous branch, M: main branch, B: lateral branch, H: hapteronous branch, t: tetrasporangium, m: tetrasporangium mother cell, c: cover cell.



*B. tenax* f. *oleophila* Post

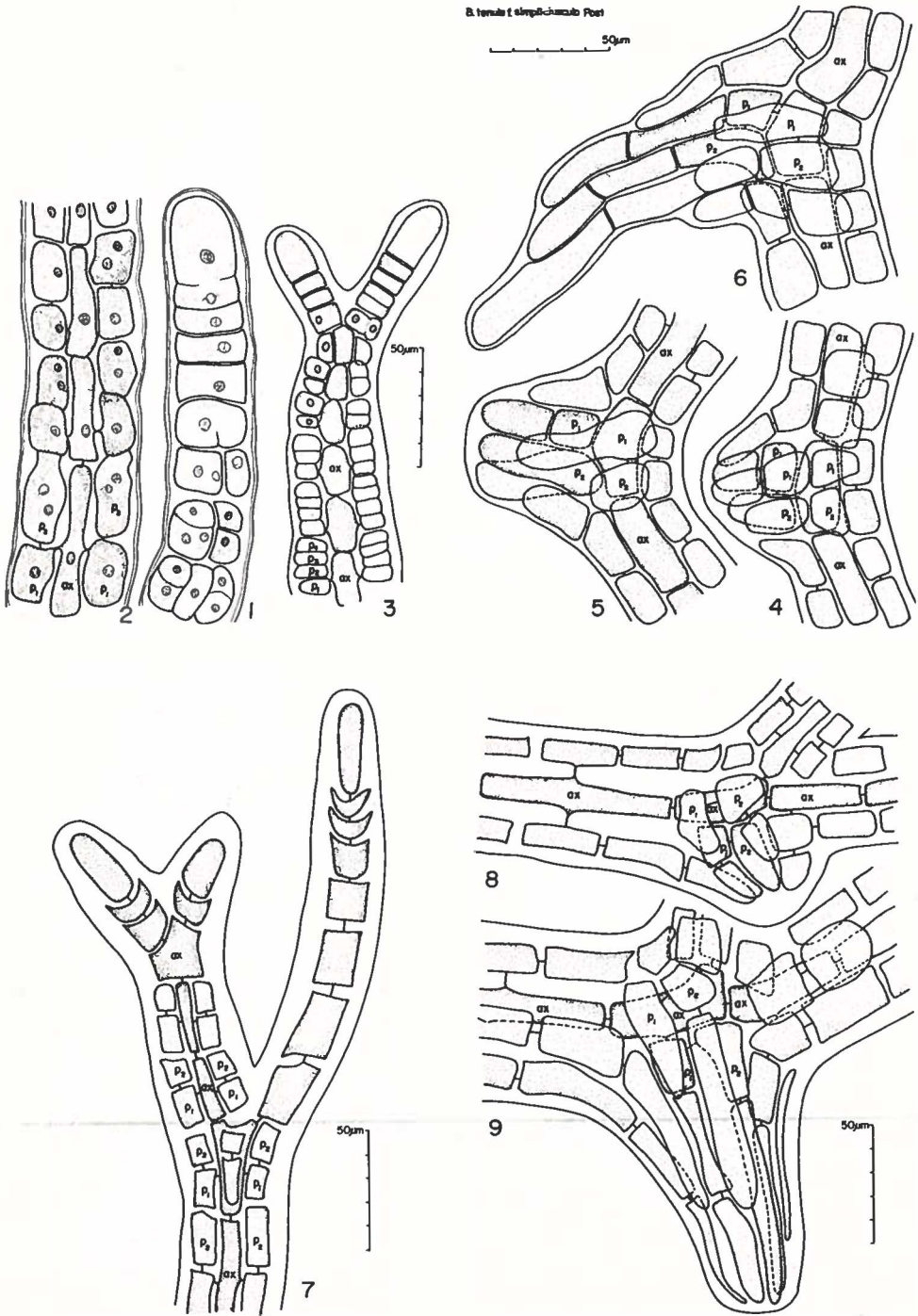
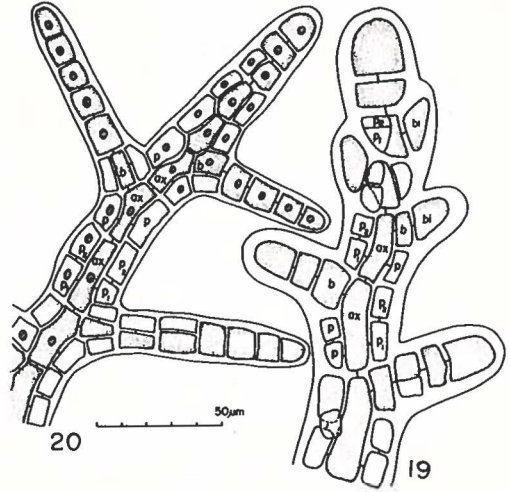
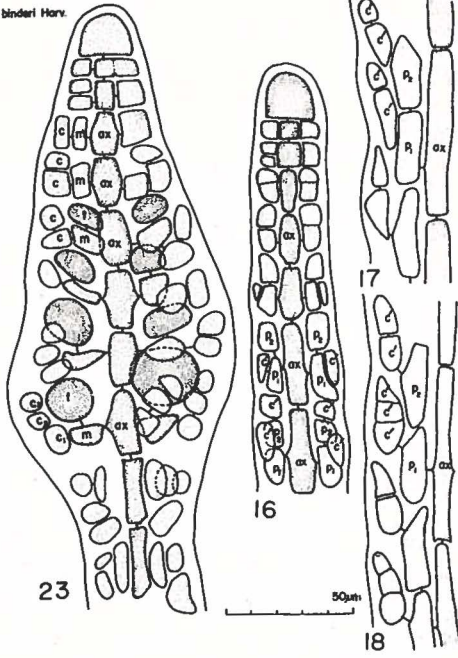


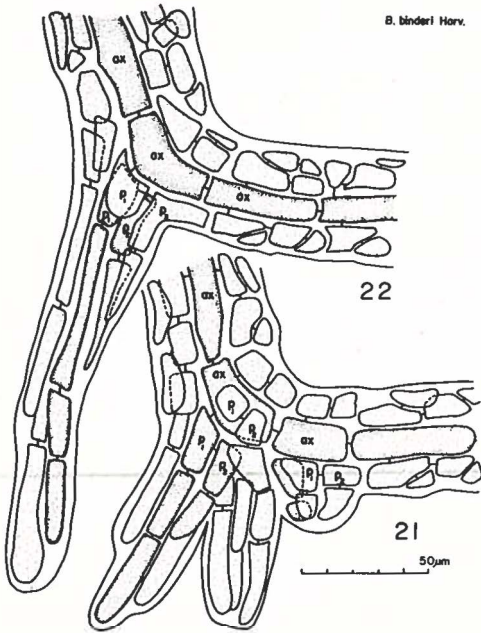
PLATE I



*B. binderi* Horv.



*B. binderi* Horv.



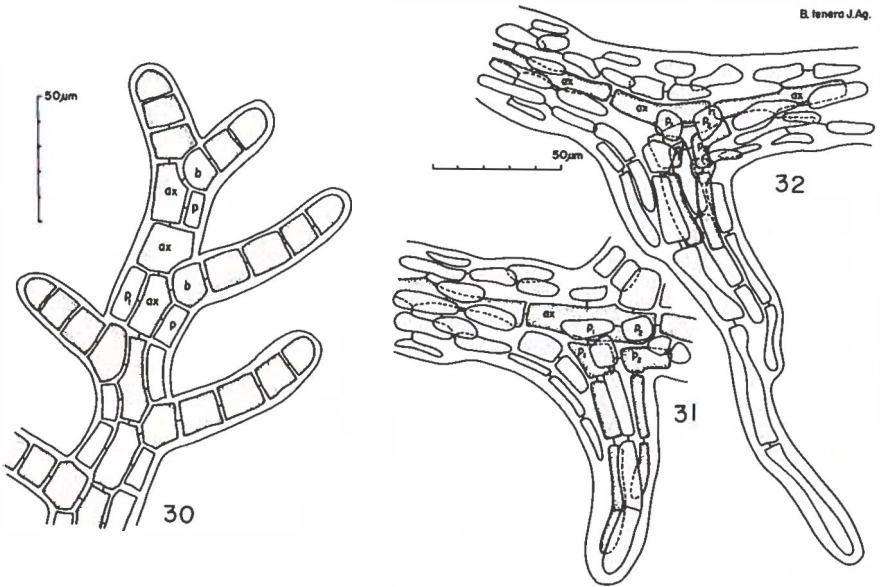
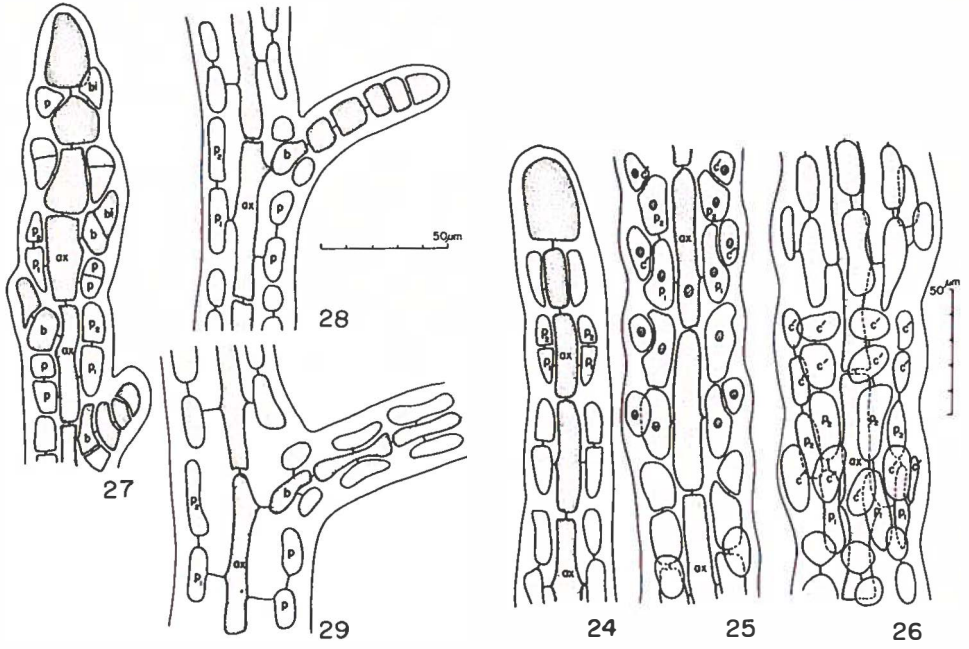


PLATE IV



*B. karonensis* Grun

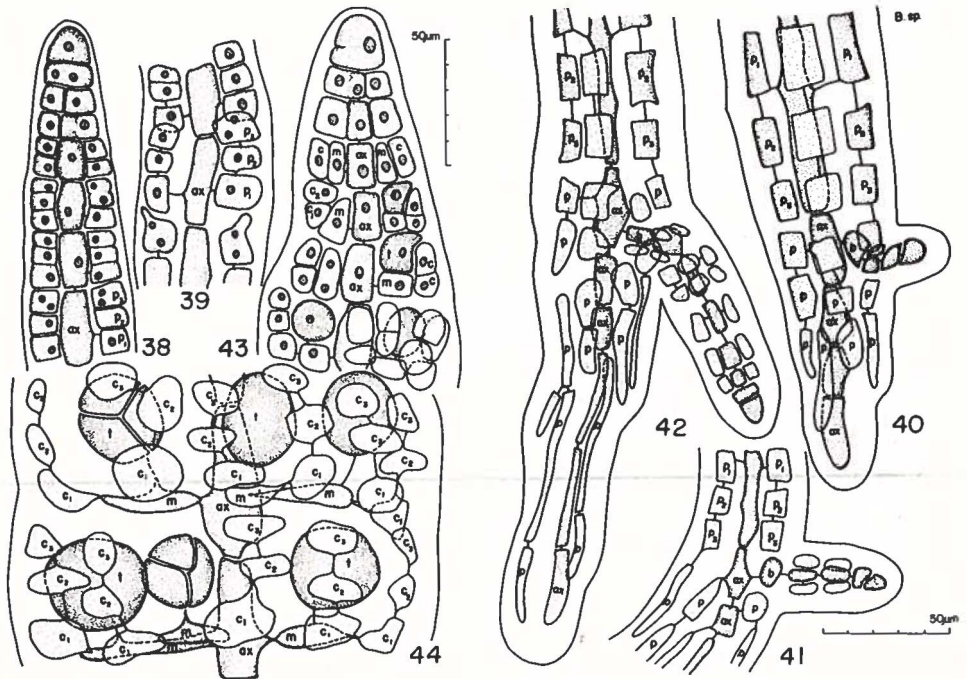
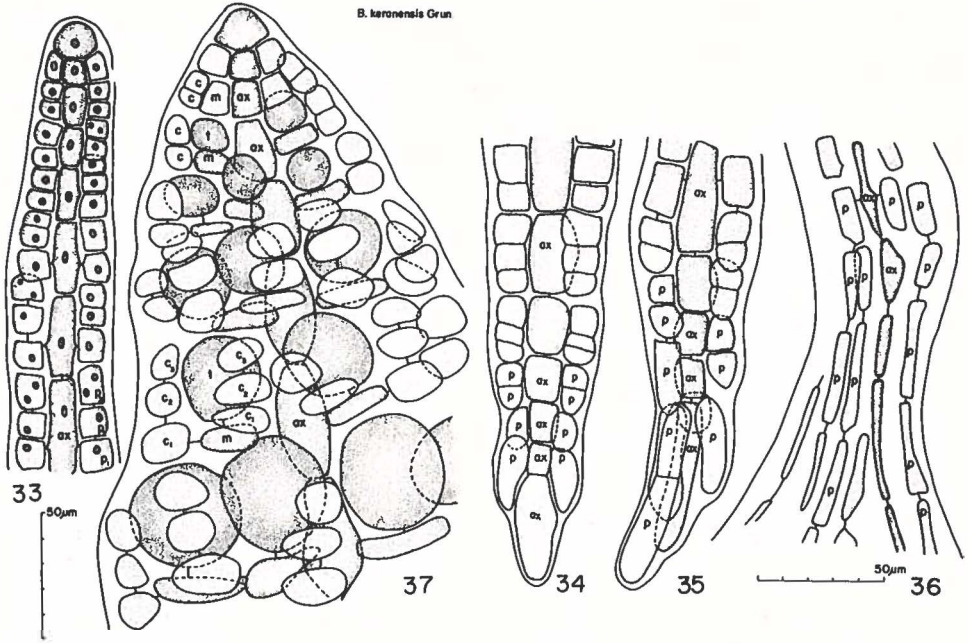


PLATE V

*B. radicans* Mont.

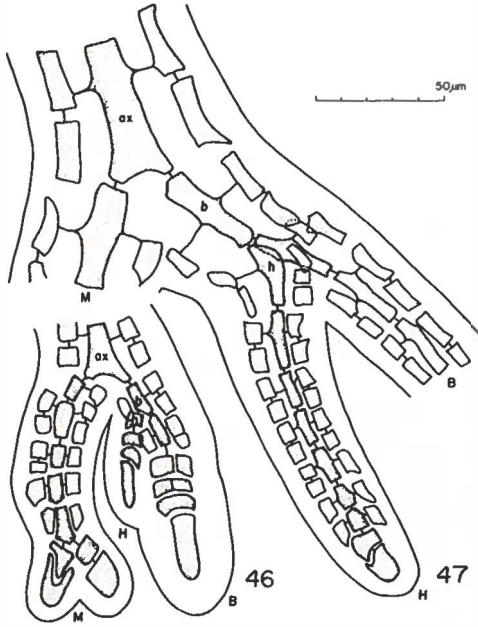
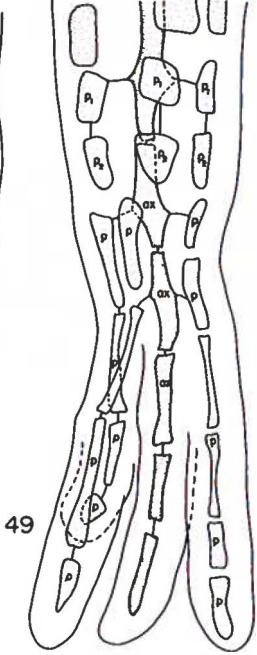
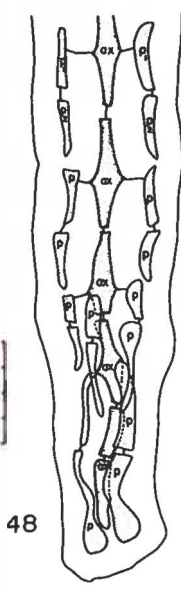
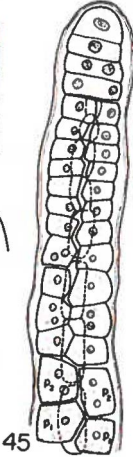
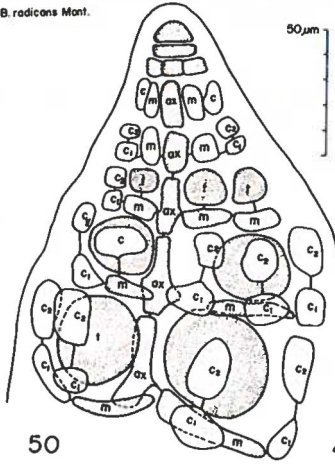
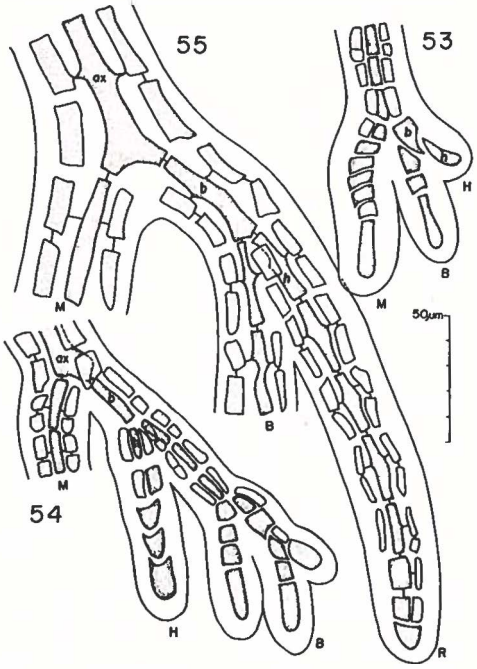
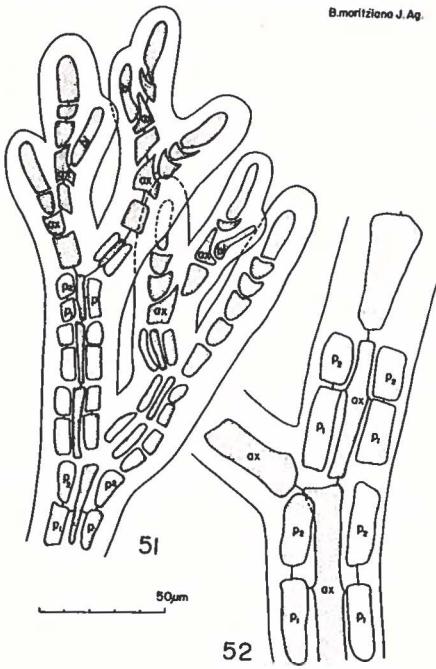


PLATE VI



*B. moritziano* J. Ag.



*B. moritziano* J. Ag.

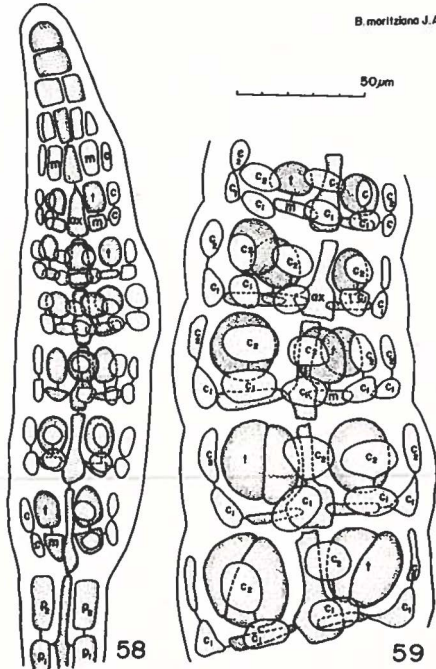
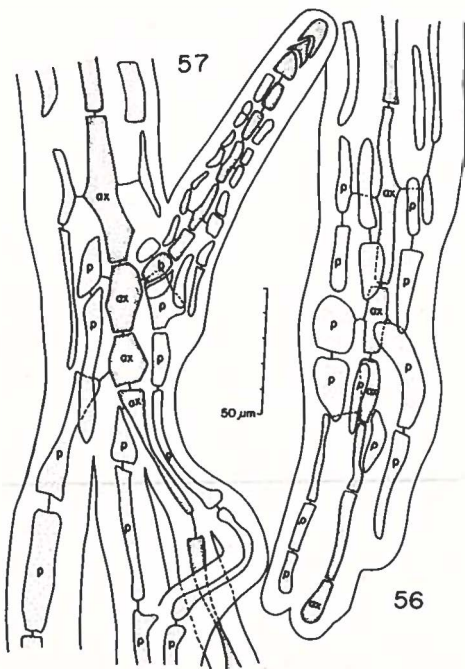


PLATE VII

