

Tropical Bryology 9: 111-116, 1994

The structure of the leaf and peristome of *Holomitriopsis laevifolia* (Broth.) H. Robins. illustrated with scanning electron microscopy.

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Abstract. The vegetative and sporophytic features of *Holomitriopsis* that distinguish this genus from *Schistomitrium* and from *Leucobryum* are discussed and illustrated using scanning electron microscopy.

Leucobryum laevifolium Broth. is an endemic of the Guyana Highlands of Venezuela and Guyana. It was described in 1901, but was rather poorly known until recently. Sporophytes were still unknown when Florschütz (1964) commented on a combination of vegetative characters in the species (leucocysts in two layers throughout the leaf and chlorocysts nearer the dorsal surface from the base to a short distance below the apex) that was "distinctive for the Malesian genus *Schistomitrium* Dozy et Molk." The lack of sporophytes prevented Florschütz from making any change of generic placement at that time.

The two genera with which *Leucobryum laevifolium* had been associated by Brotherus (1901) and Florschütz (1964) are very distinct in the form of their capsules and calyptrae. *Leucobryum* normally has capsules that are curved,

striate and strumose, cucullate calyptrae that have no fringe, and peristome teeth that are vertically striate and bifid. (One species, *L. incurvifolium* C. Mull. has erect capsules). *Schistomitrium* has capsules that are erect, smooth and cylindrical, mitrate calyptrae that have a ciliate fringe at the base and peristome teeth that are papillose and scarcely divided.

A sporophyte of *Leucobryum laevifolium* was first described by Robinson in 1965. The species differs from both *Leucobryum* and *Schistomitrium* in several features of the sporophyte, and this formed the basis for description of the new genus *Holomitriopsis* Robinson. In addition the perichaetial leaves are very elongate, clasping the base of the seta. This feature led to the generic name, from the similarity to the elongate perichaetial leaves of *Holomitrium* in the

Dicranaceae, + *opsis*, meaning to resemble. Robinson (1986) considered that *Holomitriopsis* is closely related to *Schistomitrium*.

In a recent paper Robinson (1990) surveyed the peristome structure of members of the Leucobryaceae, but *Holomitriopsis laevifolia* was omitted since the material then available was insufficient for SEM photography. Some features of the vegetative leaves were illustrated in an earlier paper (Robinson 1985.) New material from Guyana (*Henkel 68, US*) with many mature capsules in good condition has now made it possible to illustrate the distinctive sporophytic features of the genus. Further observations on the vegetative leaves are made.

Materials and methods.

Plants from the collection Henkel 68 (US) were used. Intact mature capsules were soaked in water until the operculum could be easily detached. A representative capsule was cut in half longitudinally and mounted on the SEM stub so that the outer and inner surfaces of the peristome were exposed. Vegetative leaves were soaked in water and then sectioned by hand with a razor blade. The stubs were sputter coated and then photographed using a Hitachi 520 scanning electron microscope.

Leaf structure.

The structure of the leaves was described by Florschütz (1964) as having "the leucocysts in two layers throughout the leaf and the chlorocysts nearer the dorsal side of the leaf from base to a little below the apex, where they become central." This dorsal placement is most apparent in the mid to upper regions of the leaf (Fig. 1, upper leaf section) and near the midline in the lower part of the leaf. However, towards the margin in the lower part of the leaf the chlorocysts approach the ventral (adaxial) side (Fig. 1, lower leaf section).

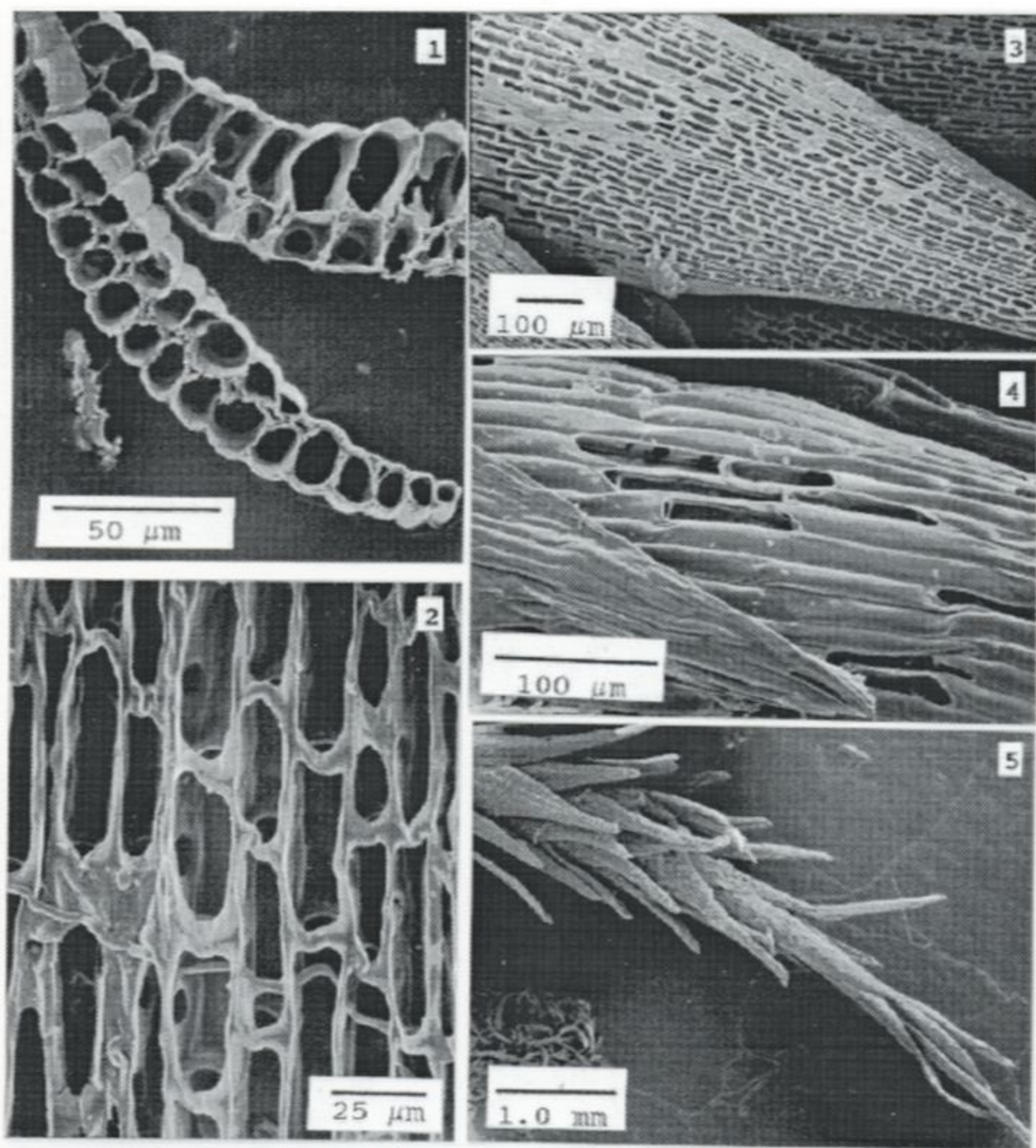
A somewhat similar leaf structure is seen in *Leucobryum martianum* (Hornsch.) Hampe ex C. Mull., which is very common in the Guianan area. In this species the dorsal and ventral

leucocyst layers are also only one cell thick, with the chlorocyst layer much nearer the dorsal surface in sections of the mid and upper leaf. However, in sections of the base of the leaf the chlorocysts are clearly closer to the ventral surface at the midline of the leaf. The two species also differ in the shape and color of the leaves. Leaves of *L. martianum* are frequently falcate-secund or somewhat spreading, with the upper leaf narrow and sub-tubulose. They also have the glossy, glaucous or whitish green color often tinged with pink or purple at the base seen in many species of *Leucobryum*. Leaves of *Holomitriopsis laevifolia* are stiffly erect to clasping, with the upper leaf acuminate with a cucullate apex, and are a matt, yellowish or reddish brown color.

In *Holomitriopsis* pores are present in the majority of the transverse walls between cells (Fig. 1), and are also present in many of the longitudinal cell walls (Figs 2, 3 and 4). The surface cells are normally intact on the ventral surface of the leaf (Fig 1), but the outer walls of the cells on the dorsal side of the leaf are frequently lost (Fig 2), with older leaves showing almost complete loss of the outer surface except in the region along the margins (Fig 3). In younger leaves few cell walls may be lost (Fig. 4). The loss of the outer cell wall appears to result from resorption of the wall material rather than by breakage, since the edges are smoothly rounded rather than fractured (see cells in Fig. 2), and may be the result of a similar process to that which forms the pores between cells. Loss of the dorsal surface cell walls occurs to a certain extent elsewhere in the Leucobryaceae (*Schistomitrium* species, *Leucobryum martianum*) but is nowhere so extensive as in *Holomitriopsis laevifolia*, where it is responsible for the matt appearance of the leaves. The remaining dorsal surface cell walls, very young intact leaves, and the ventral surface of the leaf show the characteristic iridescent highlights which contribute to the glaucous appearance of many of the Leucobryaceae.

Perichaetial leaves.

The upper leaves of the perichaetium are elongate, surrounding the base of the seta (Fig. 5). This



Figures 1-5. SEM views of vegetative leaves of *Holomitriopsis laevifolia* (Broth) H. Robins. Henkel 68 (US). 1, Cross-sections of vegetative leaves, lower section from basal region of leaf with unistratose lamina, upper section from middle region of leaf. 2, Dorsal (abaxial) surface of older leaf with surface walls resorbed, pores present in longitudinal and transverse walls of leucocysts. 3, Dorsal (abaxial) surface of older leaf with extensive resorption of surface walls. 4, Dorsal (abaxial) surface of younger leaf with few surface walls resorbed. 5, Elongate perichaetial leaves clasp base of seta. Scale on each plate.

feature is unique in the Leucobryaceae. The progressive loss of cell walls on the dorsal surface of the leaves is clearly visible.

Capsule and peristome.

The capsules are cylindrical, smooth and erect, as are those in *Schistomitrium*. However, the base of the capsule is elongate, asymmetrical and slightly twisted, with a tuberculate surface (but lacking stomates), suggesting a relationship to the curved capsules of *Leucobryum*.

The peristome teeth are variably bifid, with some teeth showing two distinct distal portions, while others are entire, with a weak median line (Figs 6, 8 and 10). In this respect *Holomitriopsis* differs from both *Schistomitrium*, with undivided peristome teeth that lack a vertical median line (Robinson 1990, Figs 14-15) and from *Leucobryum*, which has strongly divided teeth with a well developed median line.

The inner and outer surfaces of the teeth are papillose and show no sign of vertical striations (Figs 7, 9 and 10). In this respect *Holomitriopsis* resembles *Schistomitrium*, which has papillose ornamentation on both peristome surfaces (Figs 14-15, Robinson 1990). In contrast, *Leucobryum* has well developed vertical bars of the Dicranaceous type on the outer surface and papillae arranged in rows on the inner surface (Figs 10-13, Robinson 1990).

A well developed preperistome is present in *Holomitriopsis* (Fig. 7), but was not seen in either *Leucobryum* or *Schistomitrium*.

Calyptra.

The calyptra in *Holomitriopsis* is cucullate (Fig. 11), and lacks the fringe of elongated inflated unicellular hairs seen on the mitrate calyptra of *Schistomitrium*.

Dwarf males.

Dwarf males, which are common in the Leucobryaceae, are also present in *Holomitriopsis*. The plants seen were from one to four millimeters tall and showed one to three cycles of antheridia production, followed by continued

vegetative growth from a sub-apical innovation. The narrow lanceolate leaves were approximately one quarter of the size (1 mm) of those seen on non-dwarf plants. Male plants in *Schistomitrium* are similar to the females but slightly smaller (Eddy 1990.)

A further Malesian genus, *Cladopodanthus* Dozy & Molk., is very close to *Schistomitrium* and shares some further similarities with *Holomitriopsis*. Both *Cladopodanthus* and *Holomitriopsis* have two layers of leucocysts to the extreme apex of the leaf, while in *Schistomitrium* the ventral side of the leaf at the apex is filled with multi-stratose layers of cells (Eddy 1990, Magill 1993). *Cladopodanthus* also lacks a ciliate fringe on its calyptra, which is however mitrate ("oblong campanulate" Magill 1993.)

If these character states in *Schistomitrium* are considered derived (Robinson 1990, Magill 1993), the similarities between *Holomitriopsis* and *Cladopodanthus* must be considered to be plesiomorphic. Such similarity due to absence of a derived character state does not indicate any particular relationship between the two genera. Similar comments might also be made about other characters discussed.

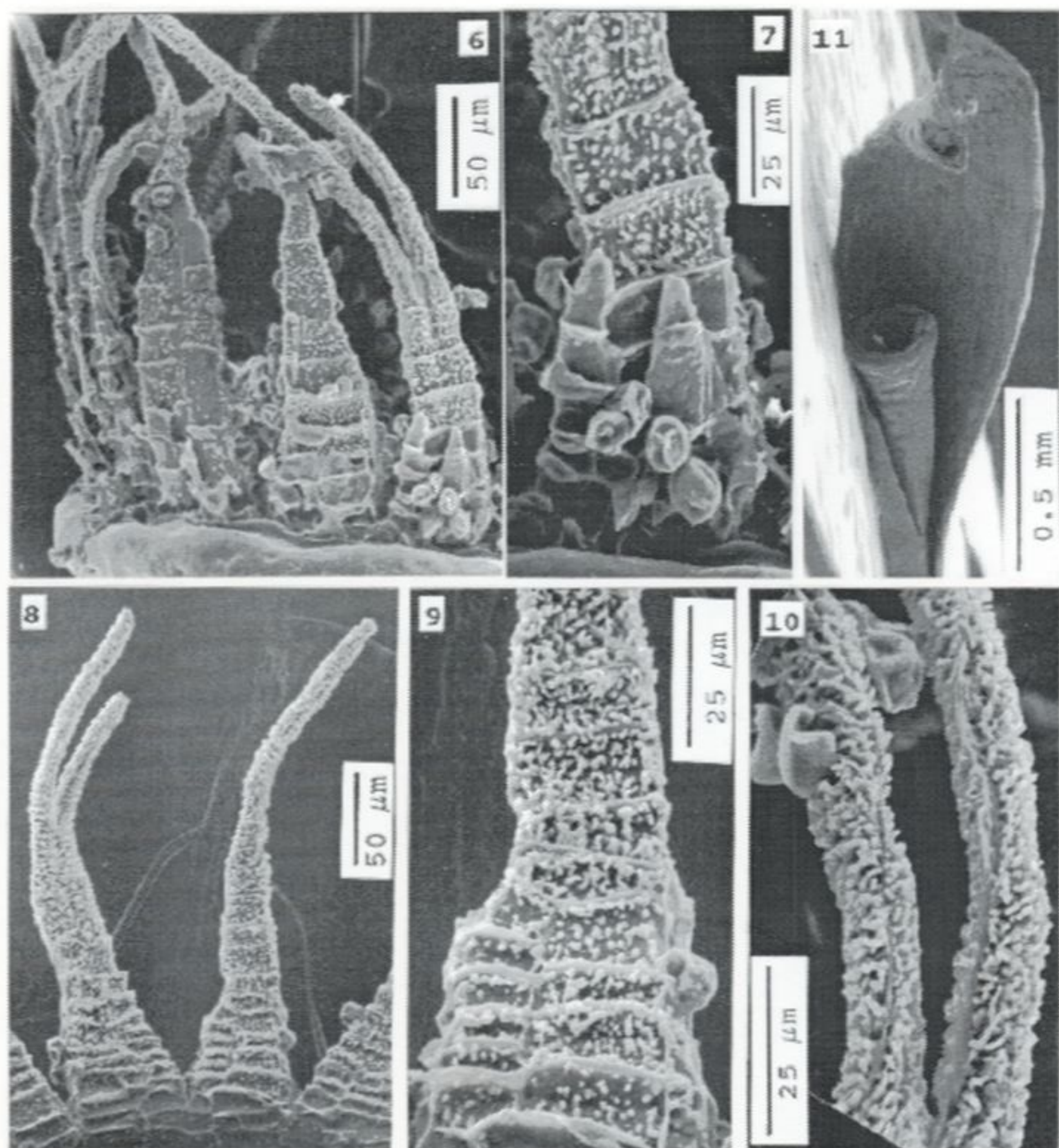
It seems clear that *Holomitriopsis*, although it shares some similarities with *Leucobryum* on the one hand, and with *Schistomitrium* and *Cladopodanthus* on the other, is quite distinct from all three genera.

Acknowledgements.

We would like to thank the Smithsonian Institution's Biological Diversity of the Guianas Project for funding support. Scanning electron negatives were taken in the SEM Laboratory at the Smithsonian Institution by Peter Viola.

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Figures 6-11. Peristome and calyptra of *Holomitriopsis laevifolia*.

6, External view of variably bifid peristome teeth, showing preperistome and distribution of papillae. 7, Detail of preperistome and papillae. 8, Internal surface of variably bifid peristome teeth with papillae. 9, Detail of papillae. 10, Densely clustered papillae on distal regions of peristome. 11, Calyptra showing absence of fringe of elongate cells. Scale on each plate.

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