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Cell wall structure of selected epiphytic mosses from a montane forest in the Venezuelan Andes

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Abstract – Cell wall cross sections of 15 mosses from a tropical lower-montane cloud forest were studied using scanning electron microscopy. The ramicolous understorey mosses, of fan, pendant and dendroid life-forms, generally have thick cell walls occupying >30% of the total cross section; the species with the thinnest cell walls, *Toloxis imponderosa*, has the leaf surface densely covered with papillae. Two basic patterns of cell wall ultrastructure are present in the understorey epiphytic mosses with hanging life forms which, along with the papillose cell walls of *T. imponderosa*, could be complementary mechanisms for water conduction and retention by pendulous mosses. Species of the forest floor and of the larger branches in the canopy, mostly of mat or turf life-forms, show relatively thinner cell walls.

Mosses / ecological adaptations / cell wall / SEM / lower montane forest / Venezuela / Andes

INTRODUCTION

Mosses are classic examples of poikilohydric organisms, meaning that the amount of water associated with them is directly linked with the availability of water from their surroundings. They have morphological adaptations and anatomical structures for internal and (especially) external water conduction, with such structures as stem central strand, papillae, mamillae, thick cell walls, julaceous habit, and a diversity of life forms (Proctor, 1984; Bates, 1998; Kürschner and Parolly, 1998). Water requirements vary depending on the habitats to which bryophytes are adapted. Some species of constantly wet places are very sensitive to drying, while others can withstand long periods of desiccation (Proctor,1984). Proctor (2002), showed that the tropical understory epiphytic species *Pilotrichella ampulacea* and *Floribundaria floribunda* from Africa have great capacity of recovery after short periods of drying and stressed the importance of their large capacity for holding external capillary water.

Schofield (1981) has pointed out that mosses from dry environments tend to have proportionately thick cell walls in relation to the protoplast. He suggested that water transport through these thickened walls might be of importance. Edelmah *et al.* (1998) showed ultrastructural adaptations of the cell wall, presumably related to water absorption in the form of mist or fog, in the moss *Rhacocarpus purpurascens* (Brid.) Paris which shows great specialisation in cell wall anatomy.

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Humid forest in temperate regions and cloud forest in the tropics are characterized by the luxuriant growth of epiphytic bryophytes (Frahm, 1990), which often thickly cover the twigs and branches of the trees and shrubs in the understorey beneath the forest canopy. In these ecosystems solitary life forms predominate (pendant, brackets, fan, etc.), which are adaptations that enhance radiation absorption and the capture and recycling of nutrients (Bates, 1998, 2000). In these shady humid habitats maximising radiation interception and nutrient acquisition (and probably also efficient scavenging of water droplets from mist and cloud) is more important than minimising water loss by evaporation. Norris (1990) pointed out that pleurocarpous hanging mosses in cloud forests are adapted to repeated cycles of drying and moistening in very short periods of time since they do not offer any resistance to drying out. Repeated cycles of hydration and rehydration could potentially be deleterious since it has been shown that bryophytes lose nutrients as a result of intermittent desiccation events. However the cell wall exchange sites provide a buffer from which cations can be later reinserted into the protoplast (Bates, 2000). The aim of this paper is to investigate cell wall adaptations of epiphytic understorey mosses compared to mosses from other habitats, and to consider their possible functional significance.

MATERIALS AND METHODS

Study site

Plant material was collected in La Carbonera–San Eusebio forest, *ca* 30 km west-north-west from the city of Mérida, Venezuela, at *ca* 8°39' N, 71°24' W, 2300-2400 m above sea level. The forest is dominated by *Rethrophyllum rospigliossi* (Pilger) De Laubenfels and is part of the lower montane forest belt (Hueck, 1978). This locality is particularly rich in vascular and non-vascular plant epiphytes (Engwald, 1999; León, 2001). For the purpose of this paper, three major habitats may be distinguished: (*1*) The canopy, the bryophytes often of turf or mat life form growing over a considerable depth of organic material; (*2*) The understorey in the trunk space beneath the canopy, with a ramicolous bryophyte cover of diverse life forms; (*3*) The forest floor, with terrestrial species sometimes ascending a variable distance up the tree bases.

Study organisms

Fifteen moss species were studied. Eleven of them are ramicolous understorey epiphytic species from La Carbonera–San Eusebio forest: *Toloxis imponderosa* (Taylor) W. R. Buck (*León 1255*), *Pilotrichella flexilis* (Hedw.) Ångstr. (*León 1468*), *Meteoridium remotifolium* (Müll. Hal.) Manuel (*León 1483*), *Squamidium leucotrichum* (Taylor) Broth. (*León 1326*), *Prionodon densus* (Hedw.) Müll. Hal. (*León 1327), Phyllogonium viscosum* (P. Beauv.) Mitt. (*León 1484*), *Adelothecium bogotense* (Hampe) Mitt. (*León 1465*), *Aptychella proligera* (Broth.) Herzog (*León 1274*), *Porotrichum mutabile* Hampe (*León 1249*), *Pterobryum excelsum* Müll. Hal. (*Pócs, León & Rico BD9713*), *Syrrhopodon gaudichaudii* Mont. (*León 1485*), *Hypopterygium tamariscinum*. (Hedw.) Brid. (*León 1247*) (a facultative epiphytic moss). For comparison we studied two terrestrial bryophytes collected from montane forest elsewhere in South America, *Thuidium tomentosum* Schimp. (*Allen 5256*) and *Trachyxiphyum subfcaltum* (Hampe) W. R. Buck (*Frahm et al. 1172*, hb. Frahm), and one species commonly found on branches in the canopy of San Eusebio forest *Holomitrium flexuosum* Mitt. (*León 1474*). All these specimens, are deposited at MERC, unless otherwise stated.

Specimens preparation for SEM

Leaves and stems of herbarium specimens were hydrated, immersed in liquid nitrogen, broken and fixed to aluminium stubs by a double side adhesive tape, and sputter coated with gold (SCD 040: Balzers Union, Wiesbaden, Germany). Leaf surface and leaf and stem transverse sections were examined in a Cambridge Stereoscan 200 SEM.

From micrographs, the total area of cell wall (in cross section) was measured, and divided by the total cross section cell area. Working from dried herbarium specimens, it was not possible to retain the lifelike appearance that could have been expected from freeze-dried or critical-point-dried fresh bryophyte material. Some of the micrographs appear to have preserved the fully-turgid form of the cells moderately well. Others, especially some of the thicker-walled species, have clearly suffered some shrinkage. While the exact values of the quotients set out in Table 1 should be treated with reservation, this does not affect the essential conclusions.

MORPHOLOGICAL ADAPTATIONS OF THE STUDIED SPECIES

As a complement to the SEM analysis, Table 2 lists some morphological characteristics of mosses living in different environments in the forest. Understorey ramicolous species show weft, pendant and dendroid life forms, while terrestrial and canopy-branch species show mat and turf life forms. Life forms are combined with characters that seem important for water storage or transport: leaf attachment and the type of alar cells (each type may relate to a different mechanisms). Leaf attachment in some understorey mosses are U shaped, a possible adaptation to hold small amounts of water in the space between the leaf and the stem. Alar cells may function as passage cells that allow rapid transport of water from the stem to the leaf. Characters such as thick outer cell layers in the stem, seem to be present in all species. Tomentum may be important in water movement or storage.

RESULTS

Scanning electron micrographs from the species *Adelothecium bogotense, Aptychella proligera, Meteoridium remotifolium*, *Pilotrichella flexilis*, *Phyllogonium viscosum*, *Prionodon densus*, *Porotrichum mutabile*, *Pterobryum excelsum*, *Squamidium leucotrichum* and *Syrrhopodon gaudichaudii* show very thick cell

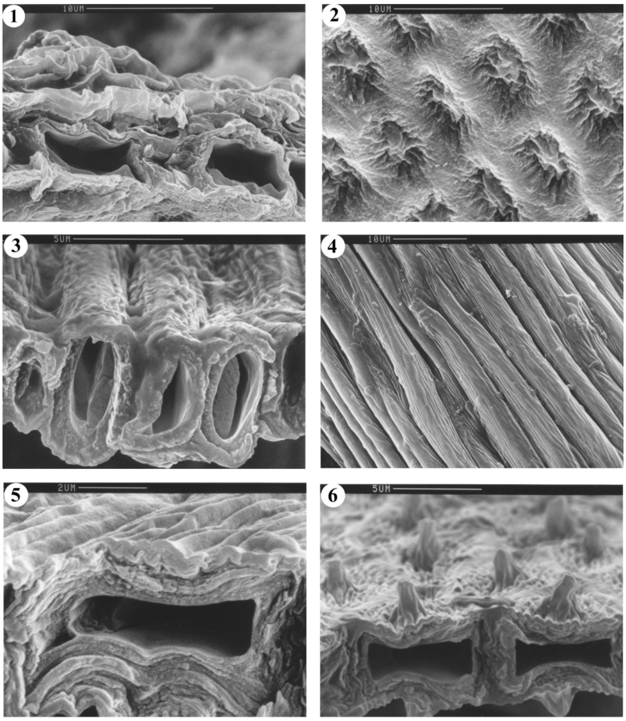
Table 1. Cell-wall area as a proportion of total cell cross section.

Species	*Cell-wall/total cross-section*
Adelothecium bogotense	0.72
Aptychella proligera	0.48
Meteoridium remotifolium	0.75
Phyllogonium viscosum	0.77
Pilotrichella flexilis	0.87
Porotrichum mutabile	0.60
Prionodon densus	0.57
Pterobryum excelsum	0.50
Squamidium leucotrichum	0.73
Toloxis imponderosa	0.33
Hypopterygium tamariscinum	0.06
Trachyxiphium subfalcatum	0.17
Syrrhopodon gaudichaudii	0.44
Thuidium tomentosum	0.27
Holomitrium flexuosum	0.12

walls. Cell walls show two types of microstructure. In one group (*Pilotrichella flexilis*, *Meteoridium remotifolium*, *Squamidium leucotrichum*, *Adelothecium bogotense*) the cell walls are composed of several very thin layers (Figs 1, 2, 5, 6, 9, 15). The second type of anatomy is present in *Aptychella proligera, Phyllogonium viscosum*, *Porotrichum mutabile*, *Prionodon densus* and *Pterobryum excelsum* (Figs 3, 7, 10, 11, 13), where the cell wall is constituted by two thick layers, the outer layer appears to be more dense and homogeneous while the inner one is porose. Between these two layers, large pores or cavities running perpendicular to the section can be observed. Often these pores can be even seen from the leaf surface (Figs 8). *Toloxis imponderosa*, (Fig. 16) is the only pendant species showing thin cell walls. Instead of thickened cell walls it has complex papillae, which form a system of channels over the leaf surface that might retain and conduct water. In contrast, the papillae of *Meteoridium remotifolium*, *Prionodon densus* (Figs 6, 12) might have no function in water retention but act as a mechanism that will avoid the leave collapsing one against the other due to the load of rainwater, thus maintaining capillary space between the leaves for water movement.

Table 2. Morphological characters of bryophytes chosen for scanning electron microscopy.

Species	*Life form*	*Leaf attach*	*Central strand*	*Axillary hairs (a.h.) or tomentum*	*Layers of thicker walled cells*	*Papillae*	*Alar cells*
Trunk epiphytes							
Toloxis imponderosa	Weft to pendant	U shape	Present	a.h.	5-7	Present	Yellow cells
Pilotrichella flexilis	Pendant	U shape concave leaves	None	a.h.	5-7	Absent	Present
Meteoridium remotifolium	Weft or pendant	U shape	Present	a.h.	2-8	Absent	Small cells
Squamidium leucotrichum	Pendant	Slightly U shape	Present	a.h.	2-8	Absent	Present
Prionodon densus	Pendant	Plane	Present	a.h. and tomentum	6-8	Present in both surfaces	Thick walled cells
Phyllogonium viscosum	Pendant	U shape auriculate, concave to cucullate	None	a.h.	3-4	Absent	Thick walled, red colored
Adelotecium bogotense	Fan	Base not U shape Costa decurrent	None	a.h.	5-7	Present or absent	Colored
Aptychella proligera	Pendant	Plane	None	a.h.	2-3	Absent	Thick walled, inflated. orange
Porotrichum mutabile	Dendroid	plane	Well differentiated		3-8	Absent	Absent or weakly differentiated
Pterobryum excelsum	Dendroid	Plane	None		6-8	Absent	Yellow, porose cells
Syrrhopodon gaudichaudii	Turf	Plane	None	Tomentum	0	Present	Large, hyaline, porose
Hypopterygium tamarascinum	Dendroid	Plane	Well differentiated		2 or less	Absent	Absent
Canopy species							
Holomitrium flexuosum	Tall turf	Plane	None	Tomentum	3-4	Absent	Extend to costa
Terrestrial species							
Trachyxiphyum subfalcatum	Mat	Plane	None	–	3-4	Absent	No
Thuidium tomentosum	Mat	Plane	None	Tomentum	3-4	Present	Yellow cells



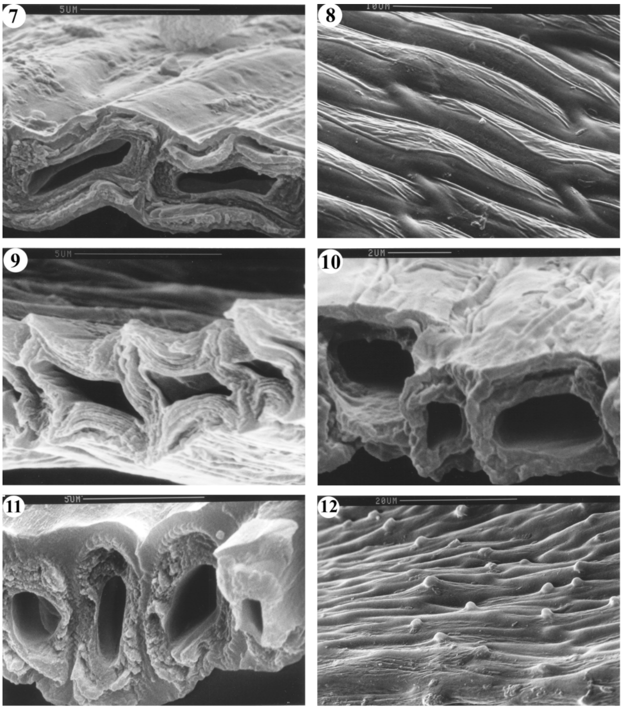
Figs 1-6. **1-2.** *Adelothecium bogotense*: leaf cross-section (1) and leaf surface (2). **3-4.** *Aptychella proligera*: cross-section of leaf (3) and view of leaf surface (4). **5-6.** *Meteorium remotifolium*: cross-section of leaf showing multilayered cell wall (5) and cross-section and surface of leaf (6).

There are thin cell walls without differentiation of layers in *Hypopterygium tamarascinum* (Figs 18-19), a species normally growing on rocks but often found as an epiphyte, in *Trachyxiphyum subfalcatum*, a species often found on rotten wood (Fig. 20), and in *Holomitrium flexuosum*, which is a common species on the upper side of branches in the canopy (Figs 26-27).

Species living in a wet or moderately wet environment (with liquid water generally present) like soil mosses such as *Thuidium tomentosum*, *Trachyxiphium subfalcatum* and *Hypopterygium tamariscinum* (all of them mats) have a similar cell wall structure to *Holomitrium flexuosum* which grows as a turf and is found in the canopy, reflecting the similarity of their water supply.

A “ridged” leaf surface observed in some of the understorey mosses *Pterobryum exelsum* (Fig. 14), *Aptychella proligera* (Fig. 4), *Phyllogonium viscosum* (Fig. 8). *Pilotrichella flexilis* and also in *Trachyxiphium subfalcatum* (terrestrial; Fig. 21) might correspond to a mechanism to carry additional external water. The relation between these structures and the external water holding capacity is still to be demonstrated.

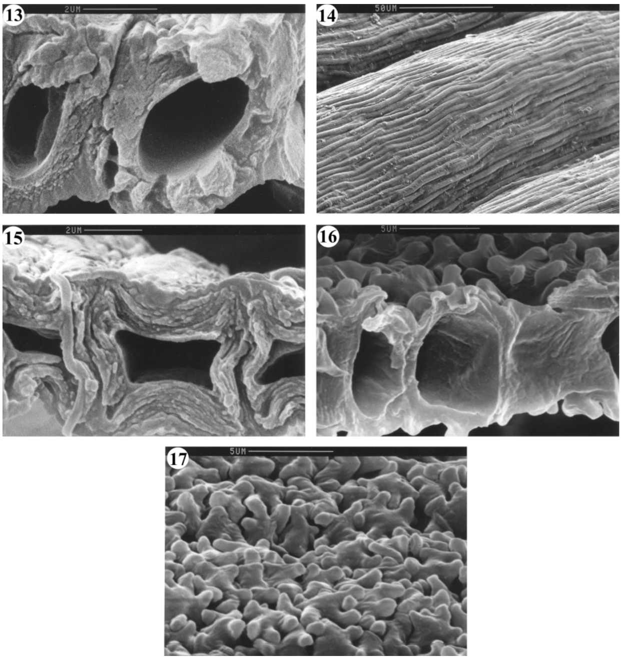
In general, in the ramicolous understorey epiphytes the cell walls make up a larger proportion of the total cross-sectional area than in the terrestrial and canopy species investigated (Table 2). The difference between the means for the two groups is highly significant (two-sample *t*-test, $P < 0.001$).



Figs 7-12. **7-8.** *Phyllogonium viscosum*: cross-section of leaf (7) and surface of leaf (8). **9.** *Pilotrichella flexilis*: cross-section of leaf. **10.** *Porotrichum mutabile*: cross-section of the leaf. **11-12.** *Prionodon densus*: cross section of leaf showing dense cell wall layer and porose cell wall layer (11) and surface of leaf (12).

DISCUSSION

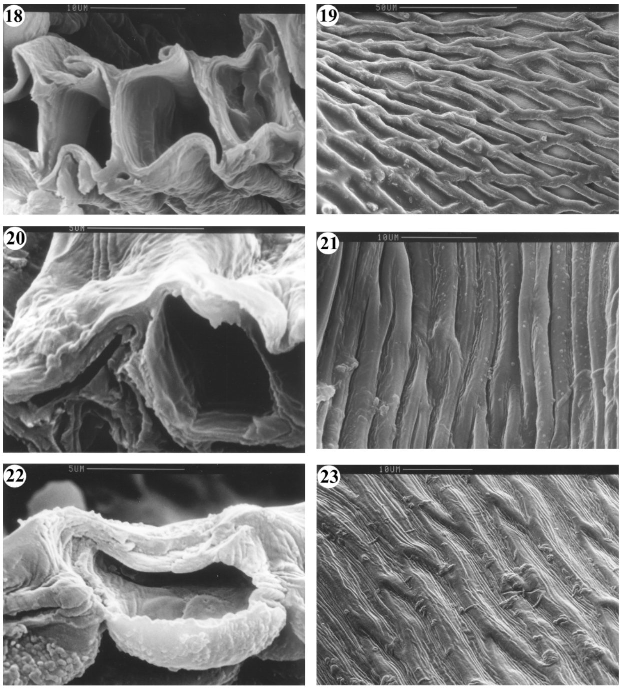
There have been many attempts to relate some morphological characters to adaptations to withstand particular ecological conditions. Kürschner & Parolly (1998) analysed anatomical characters of bryophytes growing on trunks in different forest types in northern Peru and found a correlation between adaptations such as papillae, presence of central strand, alar cells, etc., and the altitudinal gradient, bryophyte communities and their distribution patterns. Proctor (1979) examined various, mostly microscopical, features of bryophytes in relation to their physiology and ecology. Of the species studied in the present work, the pendant species *Meteorium remotifolium*, *Squamidium leucotrichum* and *Phyllogonium viscosum* have thick-layered cell walls, many of them with pores. Other species as *Prionodon densus, Aptychella proligera* and *Pterobryum excelsum* show a thick dense cell wall with pores. Layered or dense, cell walls making up a high proportion of the total cross section would hold and conduct more water apoplastically. *Toloxis imponderosa*, with thinner cell walls than the other species of this group, has the cell surface densely covered with papillae in a comparable way to the European *Anomodon viticulosus* and desiccation-tolerant



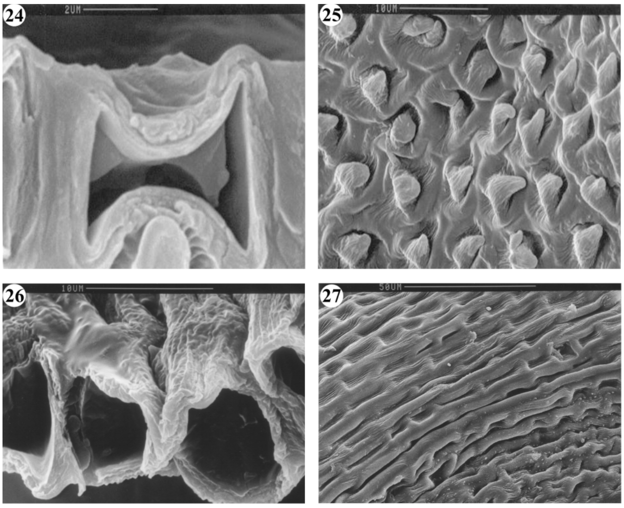
Figs 13-17. **13-14.** *Pterobryum excelsum*: cross-section of leaf showing pores (13) and leaf surface (14). **15.** *Squamidium leucotrichum*: layered cell wall. **16-17.** *Toloxis imponderosa*: cross-section of leaf (16) and leaf surface (17).

Pottiaceae illustrated by Proctor (1979), and this structure too should favour conduction and retention of water. In contrast, the cell wall of canopy species such as *Holomitrium flexuosum* (turf) and terrestrial species as *Thuidium* and *Trachyxiphium* (mats) show thin cell walls without pores and a smaller proportion of cell wall to total cross-sectional area.

It has been shown that life forms together with associated morphological characteristics are responsible for the great water holding capacity of many bryophytes (Bates, 1998). Zotz *et al.* (1997) found clear evidence of differences in the daily course of water content between life forms. Thus, in the lower-montane forest they studied in Panamá, the large dense cushions of *Leucobryum antillarum* changed relatively little in water content during the day, the smaller turf-forming epiphyte *Macromitrium cirrhosum* showed much greater fluctuations, with periods of desiccation, whilst the hanging moss *Phyllogonium fulgens* showed the greatest fluctuations of all, from 3000-4000% to less than 20% of its dry weight. Proctor (1984, 1999, 2002) has emphasised the importance of external capillary water for the maintenance of cell turgor; changes in water content from external capillary water have little or no effect on cell water potential, though large amounts of superincumbent water can interfere with gas exchange and depress carbon uptake, as Zotz *et al.* (1997) and others have noted. Fan, weft, dendroid and pendant life forms are dominant in the humid and perhumid montane belt. It is generally agreed that these life forms are efficient at scavenging water droplets from fog or mist (Frahm, 2003). The fact that ramicolous bryophytes are effective water interceptors was demonstrated by Pócs (1980). He showed that ramicolous, trunk



Figs 18-23. **18-19.** *Hypopterigium tamariscinum*: cross-section of leaf (18) and leaf surface (19). **20-21.** *Trachyxiphyum subfalcatum*: cross-section of leaf (20) and leaf surface (21). **22-23.** *Syrrhopodon gaudichaudii*: cross-section of basal part of leaf (22) and leaf surface (23).



Figs 24-27. **24-25.** *Thuidium tomentosum*: cross-section of leaf (25) and leaf surface (26). **26-27.** *Holomitrium flexuosum*: cross-section of leaf (26) and leaf surface (7).

understorey bryophytes absorb much more water than canopy bryophytes. The fan, tail and pendant life-forms of the understorey epiphytes have a greater surface for water capture, but how much water they can retain depends entirely on the detailed structure of their leaves and shoots. Proctor (2004) has emphasised that the key to understanding the adaptative niche of the pendant life form must lie in a chain of factors linked to carbon balance, including the capacity of bryophytes for extracellular water storage.

Many aspects of moss morphology and anatomy seem to be important for the water storage capability of these organisms. On the other hand, many morphological characters may simply be legacies from evolutionary history and have no significance in the present-day ecology of the species. However, it seems certain that cell wall structure is adaptively important, and that there has been much convergent evolution of this character in different taxa living the understorey of the cloud forest.

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