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Association of *Glomus tenue* (Greenall) Hall with the hepatic *Mannia fragrans* (Balb.)Frye & Clark

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Abstract

Glomus tenue (Greenall)Hall, an aseptate fungus, is found associated with the gametophyte of the liverwort *Mannia fragrans*(Balb.)Frye & Clark.Fungal hyphae mostly colonize the smooth-walled rhizoids but also scales and tuberculate rhizoids through which they pass upward into the gametophyte parenchyma of the midrib and spread from cell to cell across the wall of two adjacent cells through plasmodesmata. Vesicles develop in smooth-walled rhizoids and also in scales but not in tuberculate rhizoids. In some smooth-walled rhizoids 'false" pegs develop which are probably the entry points for nonsymbiotic fungi. Within some smooth-walled rhizoids the fungus forms branches of varying size which may be the additional sites of nutrient exchange besides the arbuscules formed within the thallus. The fungus in the thallus is mostly intracellular but rarely intercellular. In the thallus vesicles and arbuscules develop mostly within the cells of midrib. Smaller branches of old intracellular arbuscules degenerate leaving clumps of collapsed hyphae**.** The young tissue close to the growing tip and also the parenchyma cells overarching the midrib are found fungus free.

Keywords: *Glomus tenue*, *Mannia fragrans*, mycorrhiza, mycothallus, scale

Introduction

Bryophytes were previously grouped as a Division which included three classes (Rajan 2000) but at present they are classified into three separate divisions: Marchantiophyta (liverworts), Anthocerotophyta (hornworts) and Bryophyta (Mosses) (Qui et al.2006, Toritsky et al. 2007). Traditionally treated bryophytes consist of nearly 960 genera and 24,000 species (Rajan 2000). Likewise on other plants, fungi have been detected on bryophytes as their pathogens, endophytes and commensals (Davey 2006). Fungi have been found in protonema, rhizoids, cells of thallus, cells of leaves and cell organelles of bryophytes. All these structures form niches (microniches) and they offer fungi elements indispensable for their living (Dobbeler 2002).

Mosses, the largest group of bryophytes, often contain hyphae of VAM fungi (Rabatin 1980; Turnau,Ronikier and Unrug 1990). Endophytic fungal associations have also been reported in hornworts and liverworts (Duckett et al. 1991; Read et al. 2000; Ligrone et al. 2007). Almost 400 species of bryophilous fungi have been described (Ptaszynska et al.2009) but the number is very low if we consider that there probably exist 1.5 million species of fungi (Webster and Weber 2007) and each year about 1500 new species are added by scientists.

India is rich in bryophytic flora. There are about 2,489 species of bryophytes in India (Dandotiya et al.2011, Sathish et al.2013) but reports of association of these bryophytes with endophytic fungi are meagre

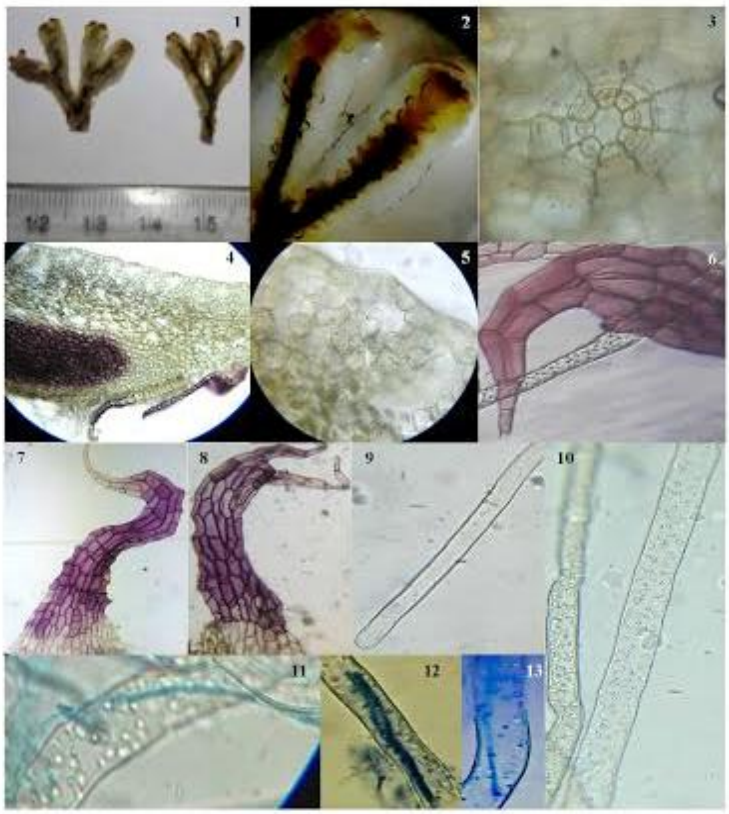
(Chaudhury and Rajaram1925; Iqbal et al. 2011; Verma and Langer 2014; Vyas et al. 2008). The present paper reports the study of interactions between *Glomus tenue*(Greenall) Hall, belonging to the family Endogonaceae (Zygomycota) (Pocock & Duckett 1984) which now belongs to the Glomeromycota (Schußler et al., 2001), and the gametophytic thallus of the liverwort *Mannia fragrans* (Balb.)Frye&Clark.

Materials and Methods

In September,2016 specimens of bryophyte *Mannia fragrans* (Balb.)Frye & Clark were collected from forest soil of Loleygaon (Eastern Himalayas), West Bengal, India. This site has an average annual rainfall of 200-250cm, relative humidity 83%, annual average temperature 11-20°C and the height from MSL (mean sea level) is 1,675 meters.

The thalli were fixed in formaldehyde/ acetic acid solution (Johanson 1940). Rhizoids and scales were separated from these fixed thalli and stained without cleaning. But the fixed thalli were washed thoroughly in running tap water for clearing adhered soil and debris from them. Hand cut sections of these thalli as well as separated rhizoids and scales were stained with 0.05% Trypan blue in lactophenol (Ligrone and Lopes 1989) for 2 minutes. The excess stain was removed by washing with lactophenol and mounted in glycerine. Slides were then sealed and photographed.

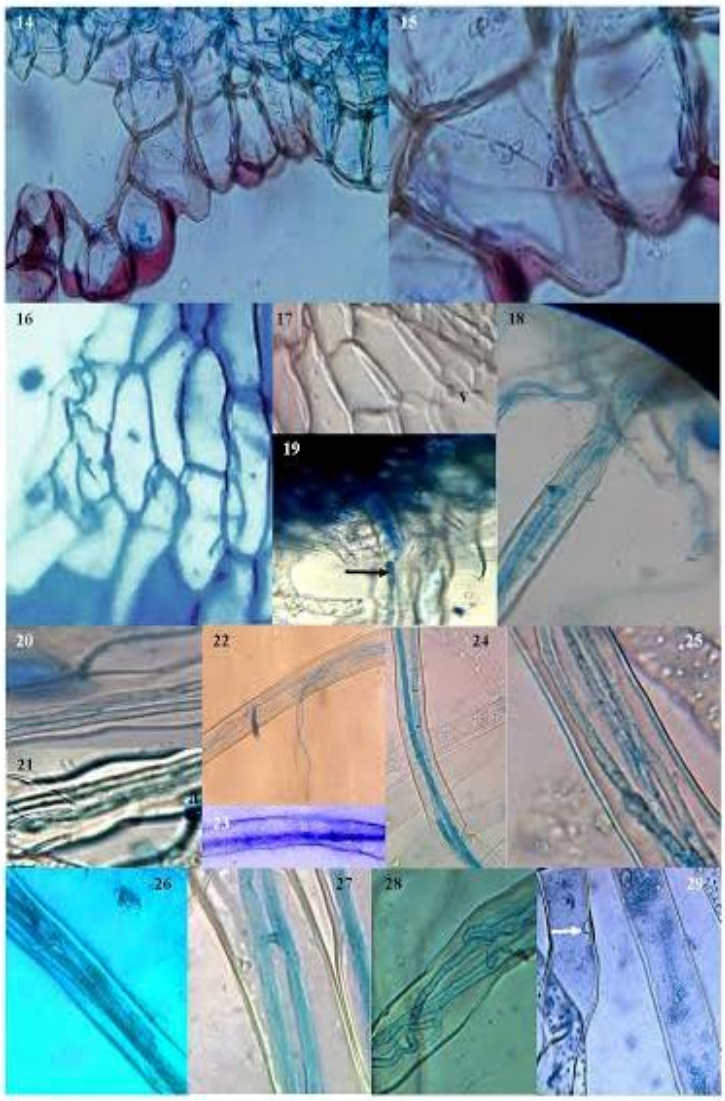
Results



Figs.1-10.*Mannia fragrans.* 1. Upper surface of thallus. 2. Lower surface of thallus. 3.Air pore. 4.T.S. of thallus. 5.Air chamber. 6 & 7.Scales with single appendage. 8.Scale with two apical appendages. 9.Smooth-walled rhizoid. 10.Tuberculate rhizoid.
Figs.11-13.Interaction of *Glomus tenue* with tuberculate rhizoids of *Mannia fragrans.* 11.Hyphae around tuberculate rhizoid. 12&13.Tuberculate rhizoids containing hyphae of *Glomus tenue.*

The bryophyte collected was identified as *Mannia fragrans* (Balb.) Frye & Clark as it possesses: (i)small (2.0-2.5cm long) and rather narrow(up to 0.5cm wide), dichotomously branched thalli without hairs at margin (Fig.1), (ii**)**scales not exteneded to margin **(**Fig.2**)** but brush of scales found at the ends of thalli as stated. Caners(2011),(iii)epidermal air pores simple, slightly elevated, surrounded by three concentric rings of 8 cells in each (Fig.3), (iv)dorsal epidermal cells thick-walled, (v) 2 rows of scales present on each side of midrib (Fig.4), (vi) air chambers small with few secondary filaments (Fig .5) or without them, (vii) scales purple to reddish, appendages may be 1(Fig.6, 7) or 2(Fig.8) with apex long, acuminate, (viii) rhizoids are of 2 types- smooth-walled (Fig.9) and tuberculate (Fig.10), (ix) dorsal side of thallus without gemma receptacle.

The tuberculate rhizoids were surrounded by hyphae (Fig.11) and were rarely invaded by some of them but formed no vesicle (Figs.12, 13).



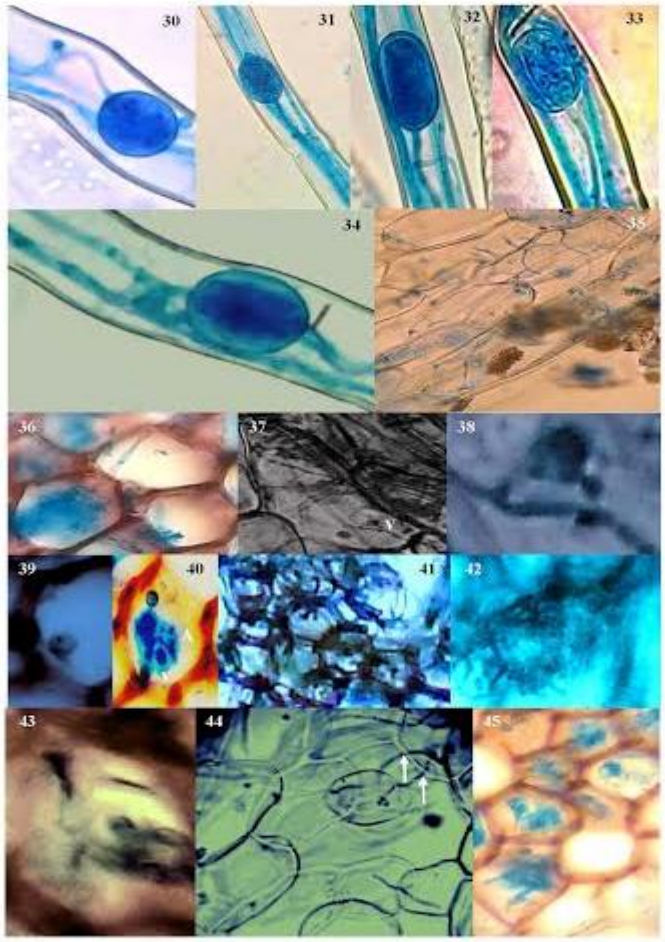
Figs.14-28. Hyphae of *Glomus tenue* within scales and smooth-walled rhizoids of *Mannia fragrans.* 14.&15.T.S.of thallus showing hyphae within cells of scale. 16.Fan shaped growth of hyphae within cell of scale. 17.Terminal vesicle in cell of scale(V). 18.Hyphae around smooth-walled rhizoid. 19&20.Entry of hyphae within smooth-walled rhizoids. 21.Appresorium (a) on surface of smooth-walled rhizoid. 22.Hyphae spreading from smooth-walled rhizoid. 23-27.Hyphae within smooth-walled rhizoids. 23.Single intracellular hypha. 24.Two intracellular hyphae, one being septate. 25.Many intracellular hyphae. 26.Intracellular hypha with Y-connection. 27.Intracellular hyphae with H-connection. 28.Intracellular hyphae with many small branches.
Fig.29.Smooth-walled rhizoid of *Mannia fragrans* with false peg (arrowed).

Scales in hand cut sections of thallus were found to contain very narrow thin–walled intracellular hyphae (Fig. 14, 15). In surface view scales show within their cells narrow hyphae with very characteristic fan-shaped growth of mycelium (Fig.16) and small vesicles (Fig. 16, 17). Some hyphae grow from scales into the thallus.

Smooth walled rhizoids show many aseptate hyphae around them and also to contain aseptate hyphae within them running longitudinally parallel to the long axis of them (Fig. 18). Smooth-walled rhizoids were found to be penetrated through any region by the fungal hyphae (Fig.19, 20). Appresorium-like structures were sometimes observed at the tip of hyphae coming in contact with the surface of rhizoids. Some hyphae were found to spread in the surrounding soil.

Smooth-walled rhizoids were frequently found to contain 1 (Fig.23), 2 (Fig.24) or more hyphae (Fig.25). Septa were rarely observed in hyphae within the rhizoids which are aged and empty i.e., devoid of cytoplasm (Fig.24). Fungus within smooth-walled rhizoids displayed Y-connection (Figs.26) and also H-connection (Fig.27). The hyphae in rhizoids often formed smaller branches (Fig. 28).

Some smooth-walled rhizoids showed formation of few ingrowths of cell wall material in the form of peg (Fig.29).



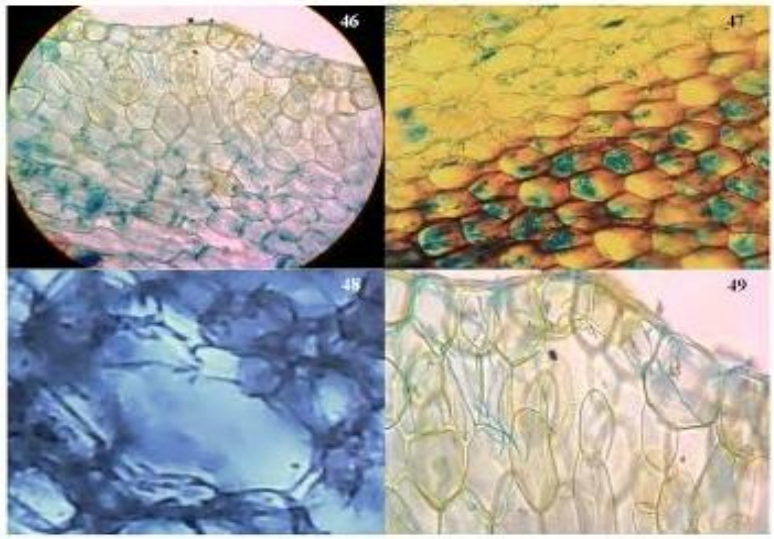
Figs.30-34.Vesicles of *Glomus tenue* within smooth-walled rhizoids of *Mannia fragrans.* 30.Spherical vesicle. 31.Oval vesicle with apical papilla. 32.Elliptical vesicle. 33.Oblong vesicle. 34.Thick-walled vesicle.
Figs.35-45.Hyphae of *Glomus tenue* within thallus of of *Mannia fragrans.* 35. Intracellular hyphae within cells of lower epidermis and a few layers above it.
36-45.Hyphae, arbuscules & vesicles within cells of midrib. 36.Intracellular hypha. 37.Intracellular hyphae and vesicle(V). 38.Enlarged view of vesicle in Fig.37. 39.Intracellular vesicle. 40.Intracellular vesicle (V) and arbuscule(A). 41.Intracellular arbuscule.42.Arbuscules forming a 'fuzz' around the main trunk hypha. 43.Intracellular hyphal ioop. 44.The hyphae passing from one cell to another across the wall of two adjacent cells through plasmodesmata (arrowed).
45. Intracellular degenerating arbuscules.

Darkly stained vesicles were found within smooth-walled rhizoids at the terminal portion of narrow hyphae which showed great diversity in shape and size. Vesicles within smooth-walled rhizoids were spherical (Fig. 30), oval with apical papilla (Fig.31), elliptical (Fig.32) or oblong (Fig.33). Cell wall of older vesicles become thickened conspicuously (Fig.34). It was also observed by Ligrone et al. (2007) in *Pellia epiphylla*(L.) Corda.

The cells of the lower epidermis and a few layers of cells above it contained only intracellular hyphae bearing branches, some of which formed loop (Fig.35).

The thick-walled cells of midrib region of thallus showed intracellular hyphae (Fig.36), intracellular hyphae and vesicle (Figs.37, 38),only vesicles (Fig.39), vesicle as well as arbuscule (Fig.40) or only arbuscule (Fig.41).

Arbuscules develop in some cells from lateral branches of the infecting hyphae (Figs.40, 41) but in some other cells arbuscules were seen as a mass of very fine dichotomously branched hyphae forming a 'fuzz' around the main trunk hypha (Fig.42).The average diameter of terminal arbuscular hyphae is 0.35-0.6µm. In some cells of this region the fungus formed intracellular coils or loops (Figs.43). The hyphae in the cells of thallus have been found to pass from one cell to another across the wall of two adjacent cells through plasmodesmata (Fig.44). It has been found that in the cells of midrib smaller branches of older arbuscules degenerate and collapse and eventually affect the whole arbuscular system resulting in formation of clumps of fungal material (Fig.45).



Figs.46-49.Hyphae of *Glomus tenue* within thallus of of *Mannia fragrans.* 46&47. Parenchyma cells overarching the midrib devoid of any mycelium. 48. Space in the photosynthetic tissue occupied by intercellular hyphae. 49.Upper epidermal cells containing narrow hyphae that running downwards up to a certain extent.

The portion beyond that extending inward up to the above of midrib region i.e., the parenchyma cells overarching the midrib were uninfected and devoid of any mycelium (Figs.46, 47).

Chlorenchyma cells of photosynthetic tissue rarely contain arbuscules and the spaces in the photosynthetic tissue are sometimes occupied by intercellular hyphae (Fig.48).

The cells of upper epidermis of thallus (Fig.49) as well as of wings have been found to contain hyphae but they do not form fan shaped structures, coils or vesicles. The upper epidermal cells contain narrow hyphae that run downwards up to a certain extent (Fig.49).The young tissue close to the growing point is free from fungus.

Discussion

Our study reveals that the hyphae invaded *Mannia fragrans* (Balb.)Frye & Clar are aseptate which indicates that it is neither a basidiomycete nor an ascomycete. Formation of vesicle and arbuscules indicates that this fungus is closely related to the phycomycetous Endogonaceae that form VAM in higher plants (Strullu 1985).The fungus shows features characterising *Glomus tenue* (Turnao et al. 1999): the mycelium shows typical fan shaped growth consisting of dichotomously branched fine hyphae of up to 2.5 µm in diameter, vesicles small of 4-9µm in diameter, strongly stained mycelium with branching and vesicles are very well developed within smooth-walled rhizoids, exceptional colonization is found within tuberculate rhizoids, from the rhizoids the mycelium spreads intracellularly into the midrib of the thallus, the hyphae sometimes form there coil-like structures, the very delicate intracellularl arbuscules are developed abundantly.

Aseptate fungal endophytes capable of forming intracellular arbuscules have been reported in a number of other Marchantiales (Strllu et al.1981, Pocock and Duckett1984). In 1999 Turnau *et al.* (1999) reported the presence of *G. tenue* in liverworts for the first time.

G. tenue is the most common symbiotic fungus in the moist places (Turnao et al. 1999).The present study area located in the Eastern Himalayas is moist and is therefore favourable abode for colonization of this fungus.

Leipina (2012) stated that the presence of arbuscules in thallus indicates functional symbiosis. As arbuscules have been found within the cells of thallus of *Mannia fragrans*, therefore the association found here may be symbiotic and mycorrhizal. Besides, according to Duckett et al. (2014) in taxa that contain symbiotic fungal endophytes, large aseptate hyphae are often visible along the entire length of rhizoids which has also been observed in the present study. But as *Mannia fragrans* does not have root, the terminology of "mycothallus" is preferred (Boullard 1988) instead of "mycorrhiza" to define its association with *Glomus tenue* belonging to Glomeromycota. However, in *Mannia fragrans* mycorrhizal colonization pattern is of 'Paris' type because here mycelium is intracellular and arbuscules develop as lateral branches from the intracellular hyphae (Smith and Smith 1996).

Some intercellular growth of hyphae of *Glomus tenue* have been observed in thallus of *Mannia fragrans* but Turnau et al.(1999)did not observe any intracellular growth of *Glomus tenue* within thallus of another liverwort *Conocephalum conicum*(L.) Dumort.

No worker has reported hyphal growth within scales of liverworts which is clearly evident in our study.

Formation of ingrowths (pegs) of cell wall material of host thallus has been reported in *Pachyschistochila splachnophylla* Engel and Schuster which presumably prevented noncampatible fungi (Pressel et al. 2008). In the present study ingrowths of wall material of cells of thallus have not been observed but in growth of cell wall materials have been reported in smooth-walled rhizoids of *Mannia fragrans*. We have not been able to ascertain their function. This type of ingrowths in smooth-walled rhizoids have been reported in *Marchantia foliacea* Mitt.and *Monoclea forsteri* Hook. by Duckett et al.(2014) who stated them as 'false pegs' associated with hyphal penetration sites. According to them entry points for non-symbiotic fungi of smooth-walled rhizoids are marked by conspicuous ingrowths of host wall material.

Direct fungal penetration through epidermal cells of thallus of *Mannia fragrans* has never been observed indicating that here the rhizoids, mostly smooth-walled rhizoids, are the access of the fungus which has also been observed in other Marchantiophytes (Ligrone et al. 2007). The fungus penetrated rhizoids at any point and formed large intracellular hyphae running in both directions as was observed in *Conocephalum conicum* and *Marchantia polymorpha* L. by Ligrone et al. (2007).Fungal colonization may affect morphology of rhizoids in hepatics (Liepina 2012) including swelling of the rhizoidal apices (Pocock and Duckett 1985) but no morphological change or swelling of apices of rhizoids have been observed in the present study. Within some rhizoids the fungus forms branches of varying size. It may be that these structures are the same as the arbuscules in the internal parenchyma. Implicit in this hypothesis is the possibility that the rhizoids in hepatics are not merely the route by which the fungus enters the host parenchyma but may also be important sites of nutrient exchange (Ligrone and lopes 1989). The observation that in several hepatics fungal infection is restricted to the rhizoids (Pocock and Duckett 1985, Duckett and Clymo 1988) supports this possibility.

After colonizing in scales and rhizoids the hyphae enter the cells of lower epidermis, a few layers of parenchyma cells above it and also in the cells of midrib. Intracellular hyphae of the cells of midrib and rarely chlorenchyma cells of photosynthetic tissue produced 'Paris' type of arbuscular mycorrhiza where arbuscules with determinate growth arise from trunk hyphae.

The hyphae pass directly from one cell to another through the cell walls of *Mannia fragrans* which was also observed in some other liverworts (Liepina 2012, Russel and Bulman 2004).

In the genus *Marchantia* upper area contains only arbuscules whereas lower area of thallus contains coils and vesicles (Ligrone et al. 2007).In *Mannia fragrans*, on the other hand, arbuscules are very rarely found in the upper area but coils, arbuscules and vesicles have been observed in the cells of midrib.

Ligrone et al. (2007) reported degeneration of arbuscules in *Petalophyllum ralfsii*(Wils.)Nees &Gottsche at a more advanced stage of colonization forming clump of collapsed hyphae which has also been observed in the cells of midrib of the thallus of *Mannia fragrans.*

The portion overarching the midrib composed of parenchyma cells are found to be uninfected and devoid of any mycelium. The possible mechanism by which the host controls the fungus is unknown. In vascular plant endomycorrhizas, the fungus only occurs in unsuberised tissues (Gianinazzi-Pearson 1984) and the host wall is thought to have a major role in the control of fungal growth (Bonfante-Fasoli 1987). A different fungus restriction mechanism must be operative in the thalli of *Mannia fragrans* since all the cells here are unsuberised.

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