Structure, Function, and Development of the Peristome of the Moss, *Rhacopilum tomentosum*, With Special Reference to the Problem of Microfibril Orientation by Microtubules

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Summary

The movement of the outer peristome teeth of the sporangium of the moss, *Rhacopilum tomentosum*, is driven by different swelling velocities of the outer ("plates") and inner ("ridges") wall thickenings due to suberin-like substances and wax-lamellae which enclose the ridges. The plates do not contain suberin-like material. The hydrophobic materials are secreted with the participation of smooth tubular ER. When the local wall thickenings of the peristome teeth are formed, microtubules are concentrated along the plasmalemma in the thickening regions. They run along the crest of the developing plates (i.e., normal to the long axis of the tooth) and parallel to the long axis in the ridge cells. The wall thickenings are composed of layers of parallel microfibrils and of matrix substances. With a few exceptions microtubules and microfibrils have different directions. Golgi vesicles, subsurface ER and coated regions in the plasmalemma also are involved in cell wall formation. The function of the microtubules is discussed.

1. Introduction

Peripheral microtubules seem to be involved in cell wall formation of plants in many cases. This has been deduced from the parallel orientation of microtubules and developing wall thickenings as in xylem elements (Hepler and Newcomb 1964, Wooding and Northcote 1964), in *Sphagnum* hyalocytes (Schnepf 1973) and in *Cobaea* seed hairs (Schnepf 1974) and also with the tips of elongating microfibrils in *Poterioochromonas* (Schnepf et al. 1975). Experiments with antitubulin agents further supported this relationship (Pickett-Heaps 1967, Hepler and Fosket 1971, Robinson et al. 1976, Robinson and Herzog 1977, Srivastava et al. 1977, Hogetsu and Shibaoaka 1978). Their role, however, is unclear. It was suggested that they shape the plasmalemma to form a mould for the developing cell wall (Schnepf 1973). Heath (1974) advanced the hypothesis that they direct polysaccharide synthetases in the plasmalemma and thus orient the microfibrils. This idea is
compatible with the results of Schnepp et al. (1975) on Poterioochromonas and of Robinson et al. (1976) and of Robinson and Herzog (1977) on Oocystis. But, as Robinson (1977) points out, "the microtubule hypothesis for microfibril orientation is still to be critisized, at least in terms of its ubiquity for all plant cells".

We, therefore, studied the development of the peristome teeth of the moss, Rhacopilum tomentosum, to ascertain whether microfibrils in a regular pattern necessarily are deposited in association with subplasmalemmal microtubules. During our studies it turned out that our results help to understand the hygroscopic movement of the peristome teeth (for reviews see Straka 1962 and Ingold 1965). Neither the electron microscopical study of Schulz and Schmidt (1974) on the development of the Funaria peristome was instructive in this respect nor the work of Maier (1973 a, b, c) which was focussed on the dehiscence of the lid of the moss capsule and on the structure and function of the anulus.

2. Material and Methods

Rhacopilum tomentosum (Hed.) Brid. grows in the greenhouses of the Botanical Garden of the University of Heidelberg. For scanning electron microscopy (SEM) we used air dried capsules.

For transmission electron microscopy (TEM) of thin sections, we fixed capsules in 0.06 M PIPES buffer with 5\% glutaraldehyde, pH 8.0, 60 minutes and subsequently with 1\% OsO$_4$, pH 6.8, 60 minutes (both at room temperature). We embedded the specimens in Spurr's mixture. In addition, we "fixed" mature peristomes with osmium vapour, dried them in a desiccator and embedded them directly. Polarizing microscopy helped to analyse the arrangement of the microfibrils.

To demonstrate the distribution and arrangement of microtubules, they are drawn in survey figures. Necessarily they are not given according to scale. This implies some incorrectness in the presentation of their exact position.

3. Results

3.1. The Structure of the Mature Peristome

3.1.1. General Structure

The peristome of Rhacopilum tomentosum consists of two rings, each ring has 16 teeth (Fig. 1). As in other Bryales, the outer and inner peristome teeth are

Figs. 1–3. SEM, mature peristome of dried capsules. Fig. 4. TEM, immature capsule
Fig. 1. Survey view, interdigitation of outer and inner peristome teeth. ×60
Fig. 2. Inner face of an outer peristome tooth with ridges. ×800
Fig. 3. Outer face of an outer peristome tooth, middle region. In the lower area the plates run normal to the axis of the tooth as in the basal zone, in the upper area the thickenings run parallel to the axis and are composed of rows of warts. The arrow labels the "divisural line", i.e., the remnant of the cell wall between the two rows of plate-cells. ×1,600
Fig. 4. Longitudinal section through the basal part of the peristome with endostomium E, plates P, and ridges R; suberized middle lamella between the plate- and the ridge-cell (arrow). ×3,000