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The ultrastructure of the placenta in *Sphagnum*

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SUMMARY

The placenta of two *Sphagnum* species was examined by electron microscopy. In contrast to all mosses so far investigated, neither sporophyte nor gametophyte placental cells of *Sphagnum* develop wall ingrowths. The sporophyte cells are highly vacuolate and the gametophyte cells close to them degenerate to produce a system of spaces filled with mucilage. Whether this type of placenta represents a primitive or derived condition in mosses is discussed.

Key words: Bryophyte phylogeny, *Sphagnum*, sporophyte–gametophyte junction, transfer cells.

INTRODUCTION

Embryophytes are characterized by a sporophyte which develops within the gametophyte and depends on it for nutrient supply. This is a very transient condition in tracheophytes, but persists for the duration of the life-cycle in bryophytes, in which the sporophyte is permanently connected to the gametophyte by a haustorial foot. A net flow of nutrients from the gametophyte to the sporophyte has been demonstrated in several bryophytes (see Ligrone & Gambardella, 1988*a*, *b* for reviews). The seat of nutrient translocation is the placenta, a region formed by the foot epidermis and the associate gametophyte tissue.

Electron microscopy of the placenta has revealed much variation between the different bryophyte groups (Ligrone & Gambardella, 1988*a*, *b*). However, a thorough appraisal of the placental structure as a useful character in clarifying the taxonomy and phylogeny of bryophytes is presently hindered by the lack of information on several major groups, including the Sphagnopsida, Andreaeopsida and Tetraphidales within the mosses.

This paper reports an electron microscopic study of the placenta in two *Sphagnum* species. The results are discussed in the context of the available information on other bryophytes.

MATERIALS AND METHODS

Plants of *Sphagnum fimbriatum* Wils. with sporophytes were collected in July from the Darmstädter Stadtwald (Darmstadt, West Germany), while laboratory-grown plants of *Sphagnum fallax* Klinggr. were obtained from Dr E. Simon (Department of Botany of the University of Kiel, West Germany).

In both species, the capsules contained nearly mature spore tetrads but the pseudopodia were unelongated. Sporophyte feet and the surrounding gametophyte tissue were excised and fixed in 3% glutaraldehyde in 0·065 M Na-cacodylate buffer, pH 7·4, for 2 h at room temperature. The specimens were post-fixed overnight in 1% osmium tetroxide in the same buffer, pH 6·8, at 4 °C, dehydrated in an ethanol series to propylene oxide and embedded in Spurr's resin. Thin sections were cut with a diamond knife, stained with 4% aqueous uranyl acetate followed by lead citrate, and observed with a Zeiss EM-109 electron microscope. For light microscopy, 3 μm-thick sections of resin-embedded material were cut with glass knives, stained with 0·05% toluidine blue in 1% Na-carbonate and photographed with a Leitz Dialux 20 EB microscope.

RESULTS

The foot of *Sphagnum* is bulbous with a nearly horizontal base and is connected to the capsule by a short seta closely invested by gametophytic tissue. In thick sections the placental region is clearly visible as an irregularly outlined region with abundant inter-

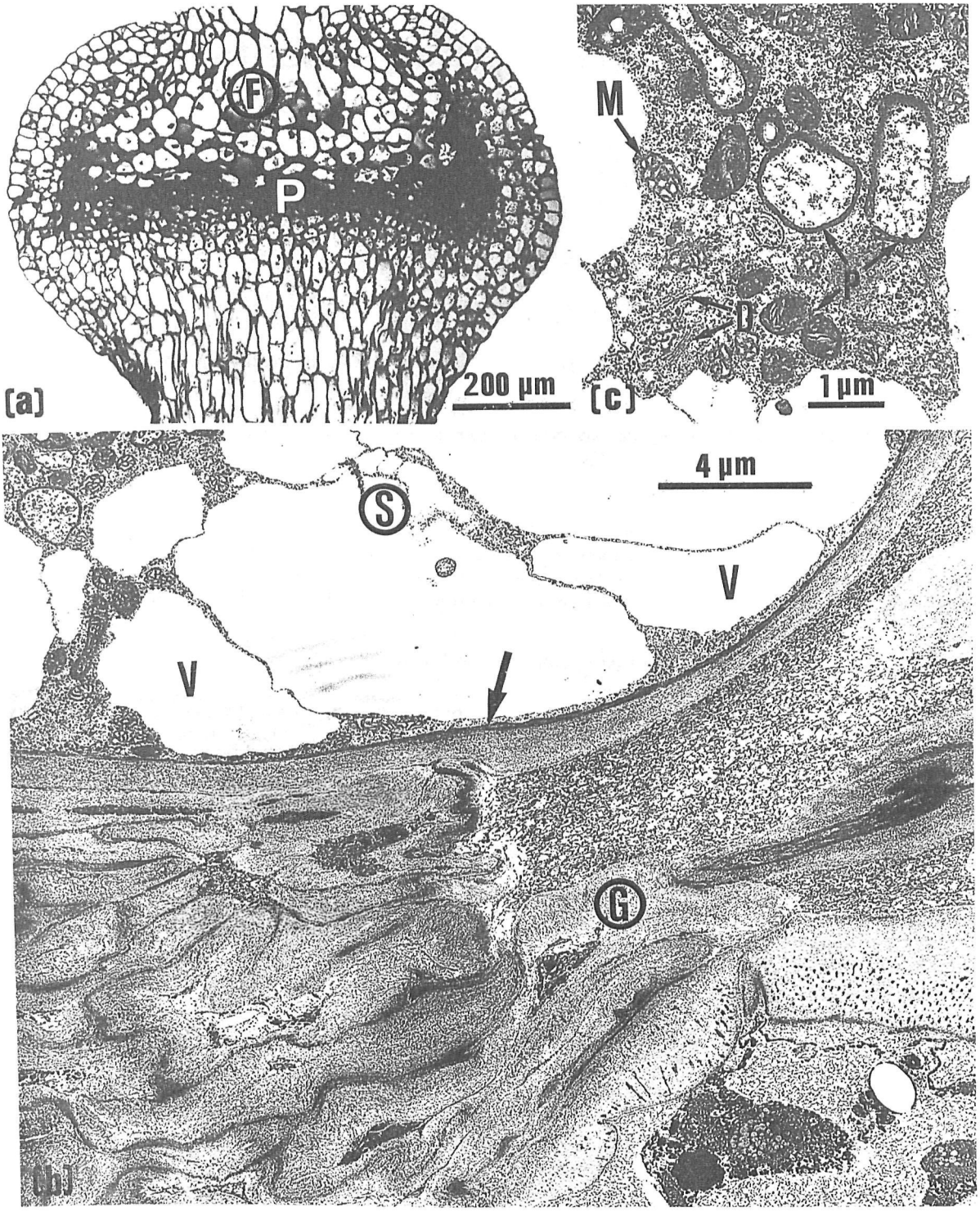

Figure 1. (*a*) The sporophyte–gametophyte junction in *Sphagnum fimbriatum*. The base of the foot (F) and the underlying gametophyte tissue form the placenta (P). Light micrograph, ×100. (*b*) Detail of the placenta in *S. fimbriatum*. A wall labyrinth is lacking in both sporophyte (S) and gametophyte (G) cells. The gametophyte cells closer to the foot have collapsed. The outer walls of sporophyte cells are covered internally by a thin layer of dense material (arrows) that is not found on the other walls. Vacuoles (V), ×6500. (*c*) Detail of sporophyte placental cell in *S. fimbriatum*. The cytoplasm is rich in ribosomes, mitochondria (M), dictyosomes (D) and pleomorphic plastids (P) with a rudimentary thylakoid system, ×13000.

cellular spaces filled with mucilage that is heavily stained by toluidine blue (Fig. 1*a*).

The placental anatomy and ultrastructure are substantially similar in the two species of *Sphagnum* examined. The sporophyte cells are much larger than gametophyte cells and often protrude into the gametophyte tissue. In *S. fimbriatum* the sporophyte placental cells contain several peripheral vacuoles

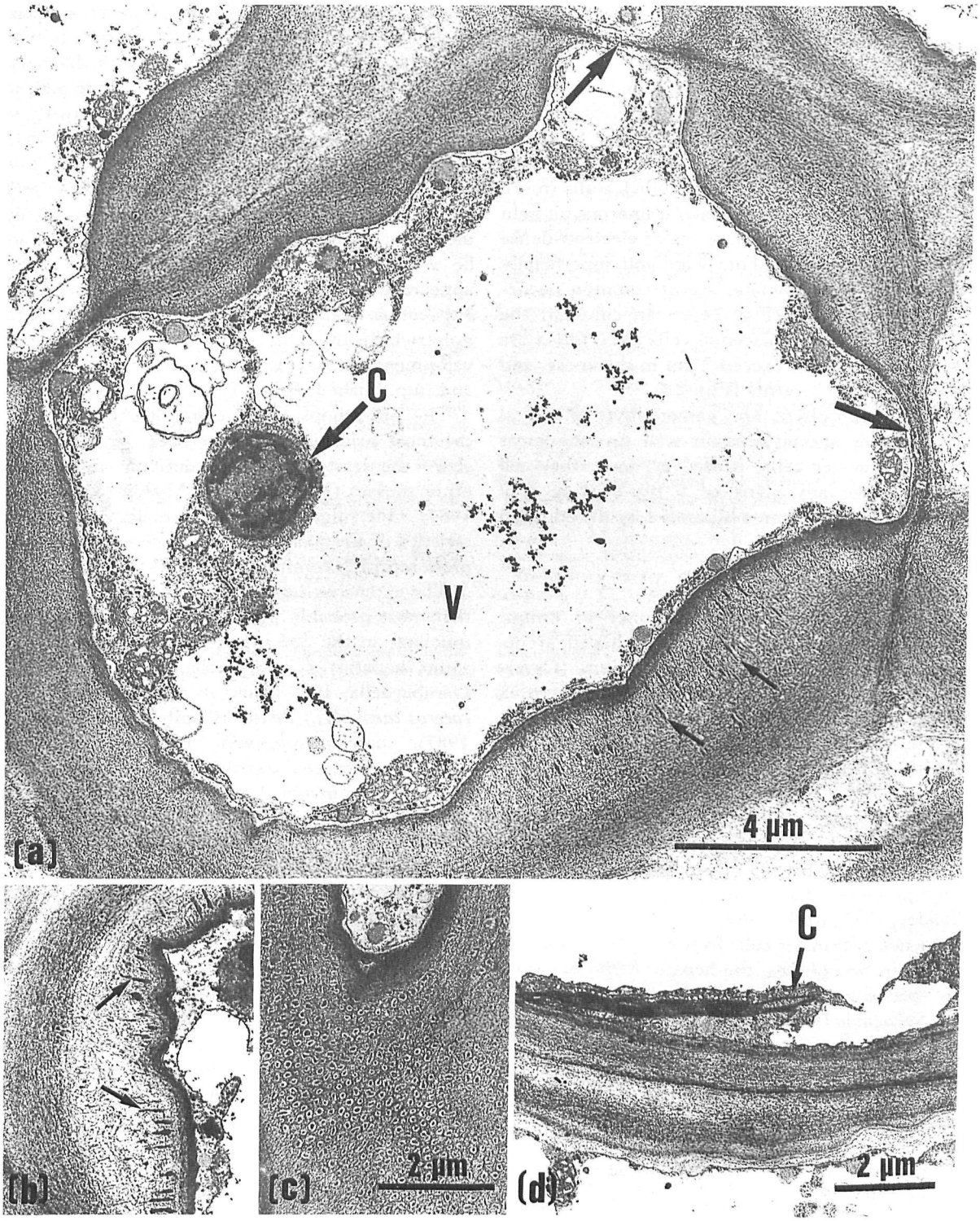

Figure 2. (*a*) Gametophyte placental cell in *Sphagnum fimbriatum*. The thick walls are locally interrupted by pits (thick arrows) and contain radially elongate deposits of dense material (fine arrows). Chloroplast (C), vacuole (V), ×9000. (*b*, *c*) Details of gametophyte cell walls of *S. fimbriatum*, showing radial deposits in longitudinal (*b* ×10000) and transverse section (*c*, ×10000). (*d*) Detail of a gametophyte placental cell in *S. fallax*. Chloroplast (C), ×8800.

with most of the cytoplasm aggregated in the centre of the cell. Cytoplasmic strands rich in organelles run between the vacuoles and connect the central cytoplasm with a thin cytoplasmic layer adjacent to the cell walls (Fig. 1*b*, *c*). Sporophyte placental cells of *S. fallax* generally contain single prominent vacuoles and very small amounts of cytoplasm close to the cell walls. In both species the walls of the

sporophyte placental cells are approx. 1 μm thick and consist of two layers differing in thickness and electron-opacity (Fig. 1*b*).

The gametophyte cells nearer the sporophyte undergo cytoplasmic degeneration and massive collapse (Fig. 1*b*), while those cells further from the sporophyte remain alive. These latter cells in *S. fimbriatum* possess exceedingly thick walls (more than 4 μm) with wavy profiles and numerous pit field areas (Fig. 2*a*). Rod-like deposits of electron-dense material, approx. 80–150 nm wide and superficially resembling plasmodesmata, are of common occurrence in these walls (Fig. 2*b*, *c*). In contrast, the walls of gametophyte placental cells of *S. fallax* are more uniform, rarely exceed 2 μm in thickness, and lack dense radial deposits (Fig. 2*d*).

Neither sporophyte nor gametophyte placental cells of either species contain wall protuberances typical of transfer cells. Moreover, in neither cell type are there any signs of a pre-existing wall labyrinth having become obliterated by the addition of new wall material.

DISCUSSION

The Sphagnopsida exhibit a number of unique characteristics, including the dome-shaped archesporium arising from the amphithecium (Cavers 1911), spore-wall layering (Brown, Lemmon & Carothers, 1982), and sperm architecture (Duckett, Carothers & Miller, 1982), that warrant their separation from the remainder of the mosses (Anderson, 1980; Scagel *et al.* 1982). The isolation of the Sphagnopsida is reinforced by the lack of transfer cells from either side of the placenta in the two species examined here. This finding is in agreement with previous light microscopic observations (Blaikley, 1933; Roth, 1969; Gunning & Pate, 1974).

Absence of transfer cells from the placenta is very unusual in bryophytes, the hepatic *Pellia* being the only species known to date that shares this feature with *Sphagnum* (Gunning & Pate, 1974). Within the mosses, transfer cells are restricted to the sporophyte in the Polytrichales (Ligrone & Gambardella 1988*a*, and unpublished data) and perhaps in members of the Andreaeopsida (Blaikley, 1933; Roth, 1969), whereas they are present on both sides of the placenta in the Buxbaumiideae and Eubryideae (Ligrone & Gambardella, 1988*a*).

It was not possible, in the present study, to examine *Sphagnum* sporophytes at an earlier developmental stage. However, it seems quite unlikely that the absence of transfer cells in the mature material we examined might be a result of a secondary removal of the wall ingrowths. Obliteration of the wall labyrinth occurs during late developmental stages in placental cells of mosses (Browning & Gunning, 1979), liverworts (Gambardella, 1987), and anthocerotes (Gambardella & Ligrone, 1987), but it is caused by the addition of new wall material which fills the spaces among the wall ingrowths. This process results in the formation of thickened walls in which the contours of the pre-existing ingrowths remain clearly visible. By contrast, the sporophyte placental cells of *Sphagnum* exhibit thin walls at maturity and no signs of pre-existing ingrowths are discernible in the thick walls of gametophyte placental cells. These walls, because of their loose texture, probably create a low resistance pathway for water and solute movement (Trachtenberg & Zamski, 1979). It may be worthy of note that thick walls with similar appearances occur in gametophyte placental cells of *Pogonatum aloides* (Hedw.) P. Beauv. and in other polytrichaceous mosses even at very young developmental stages (Ligrone & Gambardella, 1988*a*, and unpublished data).

The Sphagnopsida are commonly thought to be the most primitive extant mosses, or at least they share the least number of derived features with other mosses (Kumar, 1984; Mishler & Churchill, 1984). One might conclude from this that characteristics of the placenta of *Sphagnum* represent the plesiomorphic condition.

The extensive degeneration of gametophyte cells, that most probably produces the spaces filled with mucilage in the *Sphagnum* placenta, also occurs in some hepatics (Gambardella, 1987; Ligrone & Gambardella, 1988*a*) and in the anthocerote *Phaeoceros laevis* (L.) Prosk. (Gambardella & Ligrone, 1987), thereby suggesting its primitive nature. However, because the evolution of the Sphagnopsida has probably involved extensive reduction, such as the loss of the leaf nerve, seta, and conducting tissues (Mishler & Churchill, 1984, 1985), the evolutionary loss of placental transfer cells cannot be ruled out.

There is compelling evidence in support of the idea that the hydroids and leptoids of mosses are homologous with the tracheids and sieve elements of tracheophytes (Hébant, 1977; Scheirer, 1980), and were already present in the common ancestor of mosses and tracheophytes (Mishler & Churchill, 1985; Edwards, 1986). The occurrence of highly differentiated conducting tissues in the Polytrichales would therefore be considered plesiomorphic. If so, it seems likely that, because of the close relationship between the conducting system and placenta in mosses (Ligrone & Gambardella, 1988*a*, *b*), a primitive placenta has been retained along with conducting tissues in polytrichaceous mosses. Accordingly, the presence of transfer cells in the placenta of other embryophytes, including hepatics and anthocerotes (Ligrone & Gambardella, 1988*a*, *b*) as well as ferns (Gunning & Pate, 1969), suggests that the *Sphagnum*-type of placenta may not be truly primitive.

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