Acta Bot. Neerl. **41**(1), March 1992, p. 31–42

The development of mucilage cells in *Hibiscus schizopetalus*

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SUMMARY

The development and (ultra-)structure of mucilage cells in the shoot apex and leaf in *Hibiscus schizopetalus* (Mast.) Hook.f. is described. In the shoot apex, mucilage cells mostly develop simultaneously in pairs. The mucilage was initially deposited as a layer between the plasma membrane and the cell wall. After prolonged mucilage deposition, the remaining cytoplasm was located in the centre of the cell, where it degenerated. At maturity, several mucilage cells arranged in one line, showed local breakdown of their common cell walls, and thus formed a canal or cavity which was surrounded by a sheath of smaller neighbouring cells. In the mesophyll, mucilage cells were present underneath the veins. The development was similar to that of mucilage cells in the shoot apex. Finally, several mucilage cells were aligned parallel to the vein and, after local cell-wall breakdown, fused with each other forming a kind of canal. Mucilage cells in the adaxial epidermis deposited mucilage against the inner, peripheral cell-wall. Upon prolonged mucilage deposition, the cytoplasm remained at the outer peripheral wall of the cells. In none of the mucilage cells of *Hibiscus schizopetalus* was a suberized layer detected in the cell wall. The differences between mucilage cells of the Malvaceae and those of the Lauraceae and Annonaceae are discussed.

Key-words: development, *Hibiscus schizopetalus*, leaf, mucilage cell, shoot apex.

INTRODUCTION

Among the Dicotyledons that contain mucilage cells or cavities, the Malvales constitute the most well-known order. In the Malvaceae, most species studied contain mucilage cells, cavities and ducts in every organ (Metcalfe & Chalk 1965; Gregory & Baas 1989).

Most studies on mucilage cells in leaf and stem in the Malvales were made using light microscopy (Trécul 1866; Walliczek 1893; Nestler 1898; Spegg 1959, Nabeesa & Madhusudanan 1984). Ultrastructural reports exist for *Althaea* (Bouchet 1971; Bouchet & Deysson 1976). *Tilia* (Bouchet 1973) and *Sterculia* (Bouchet & Deysson 1974). *Hibiscus* has not been studied in detail. One report is known of a light microscopical study of the leaf (Rao & Ramayya 1984) and two studies deal with fruits (light microscopy: Scott & Bystrom 1970; transmission electron microscopy: Mollenhauer 1967).

In this report we describe the development of mucilage cells in *Hibiscus schizopetalus* (Mast.) Hook.f. (Malvaceae), and compare the mucilage cells with those in so-called

'primitive' dicotyledonous families such as Lauraceae and Annonaceae, in which the oil and mucilage cells presumably develop as homologues (Baas & Gregory 1985; Bakker *et al.* 1991).

The present paper presents results of light- and electron microscopical investigations of the development of mucilage cells in the shoot apex and leaf of *Hibiscus schizopetalus*.

MATERIALS AND METHODS

Light microscopy

Fresh, fully developed leaves of a shrub of *Hibiscus schizopetalus*, growing in the tropical greenhouse of the Hortus Botanicus in Leiden, were fixed in FAPA (= mixture of formalin, alcohol, propionic and acetic acid) and sectioned in water or 96% alcohol to prevent the dissolution of oil or mucilage respectively. The sections were stained with chrysoidin/acridin red (1% in water) for lipophilic compounds or with alcian blue (1% in 70% alcohol) for mucilage (Richter 1977).

Longitudinally cut pieces of the shoot apex and small pieces of mature leaf were fixed in glutaraldehyde/paraformaldehyde and OsO_4 and embedded in Epon (Bakker & Gerritsen 1989). Serial 1 μm sections were stained with toluidine blue O.

Fluorescence microscopy

Thick (30 μm) transverse leaf sections (fixed in FAPA) were embedded in glycerin–gelatin on cover slips and examined for autofluorescence.

Other sections were stained in berberin-hemisulphate (0·1% in water), washed and subsequently counterstained in anilin blue (0·5% in water) for the detection of suberin (Brundrett *et al.* 1988). Both types of fluorescence in the sections were examined with a Leitz Laborlux fluorescence microscope using a DAPI (A) filter.

Transmission electron microscopy

Young shoot apices, including a few surrounding developing leaves, and small parts of mature leaves were processed for TEM as described by Bakker & Gerritsen (1989). Ultrathin (90 nm) sections were stained with uranyl acetate and lead citrate.

RESULTS

Mucilage cells in the shoot apex and mesophyll

Light microscopy. In the cortex and pith of the shoot apex, mucilage cells were mostly present in pairs. The cells of each pair were oriented parallel to the long axis of the stem, and in approximately the same developmental stage (Fig. 1a–d). Mature mucilage cells were also seen aligned in a row of more than two cells thus forming a kind of canal (Fig. 1e).

The mucilage cells in the mesophyll were observed mostly as mature cells characteristically positioned underneath the minor veins (Fig. 2b), aligned in a row, forming a canal-like cavity in a parallel position to the vein (Fig. 2c). In cross sections the 'canals' were approximately 50 μm wide, 35 μm high (Fig. 2b) and in most cases approximately 100 μm in depth. Sometimes a full mature 'canal' reached a length of *c.* 200 μm. Only few mucilage cells representing earlier developmental stages were observed (Fig. 2a).

The following developmental sequence is based mainly on observations in the shoot apex. Very young (mucilage) cells, possessing a large central vacuole and parietal cytoplasm were distinctly larger than the surrounding cells (Fig. 1a) and were observed from

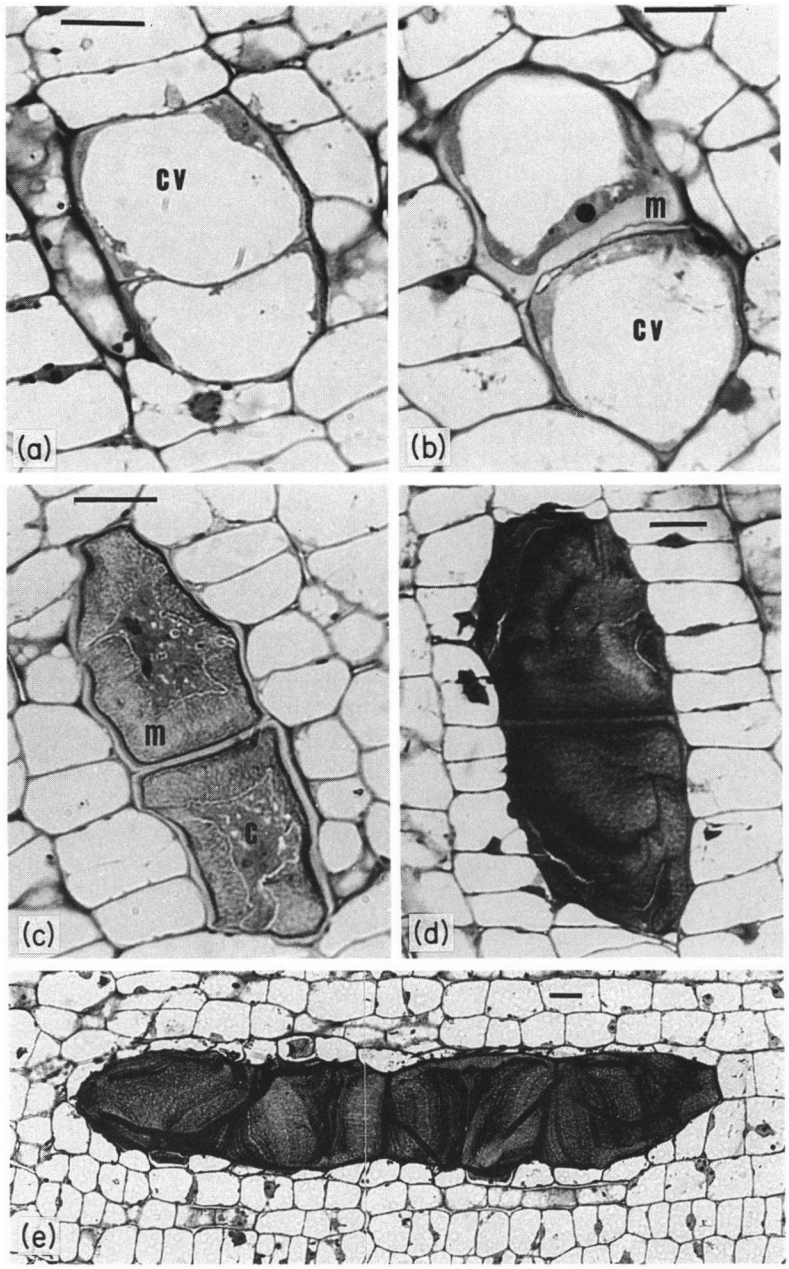

Fig. 1. *Hibiscus schizopetalus.* Light micrographs of the shoot apex. 1 μm longitudinal sections stained with toluidine blue. a–d: longitudinal axis of the stem runs from the lower right side towards the higher left side. (a) A pair of very young mucilage cells apparently in the same developmental stage. The cells are larger in size than surrounding cells and show characteristic parietal cytoplasm and central vacuole. Bar = 20 μm. (b) Pair of young mucilage cells. Mucilage is deposited as a thin layer between cell wall and plasma membrane. The central vacuole is still present. Bar = 20 μm. (c) Mucilage cell pair with degenerating cytoplasm after prolonged mucilage deposition. Bar = 20 μm. (d) Fully mature mucilage cell pair filled with mucilage. Bar = 20 μm. (e) A mucilage 'canal' consisting of several aligned mucilage cells with local cell-wall breakdown, completely filled with mucilage. Longitudinal axis of the stem runs from the right to the left. Bar = 20 μm.

Abbreviations used: c = cytoplasm; cv = central vacuole; d = dictyosome; ep = epidermis; m = mucilage; mc = mucilage cell; mi = mitochondrion; p = plastid; s = starch granule; sc = sheath cell; vb = vascular bundles; w = cell wall.

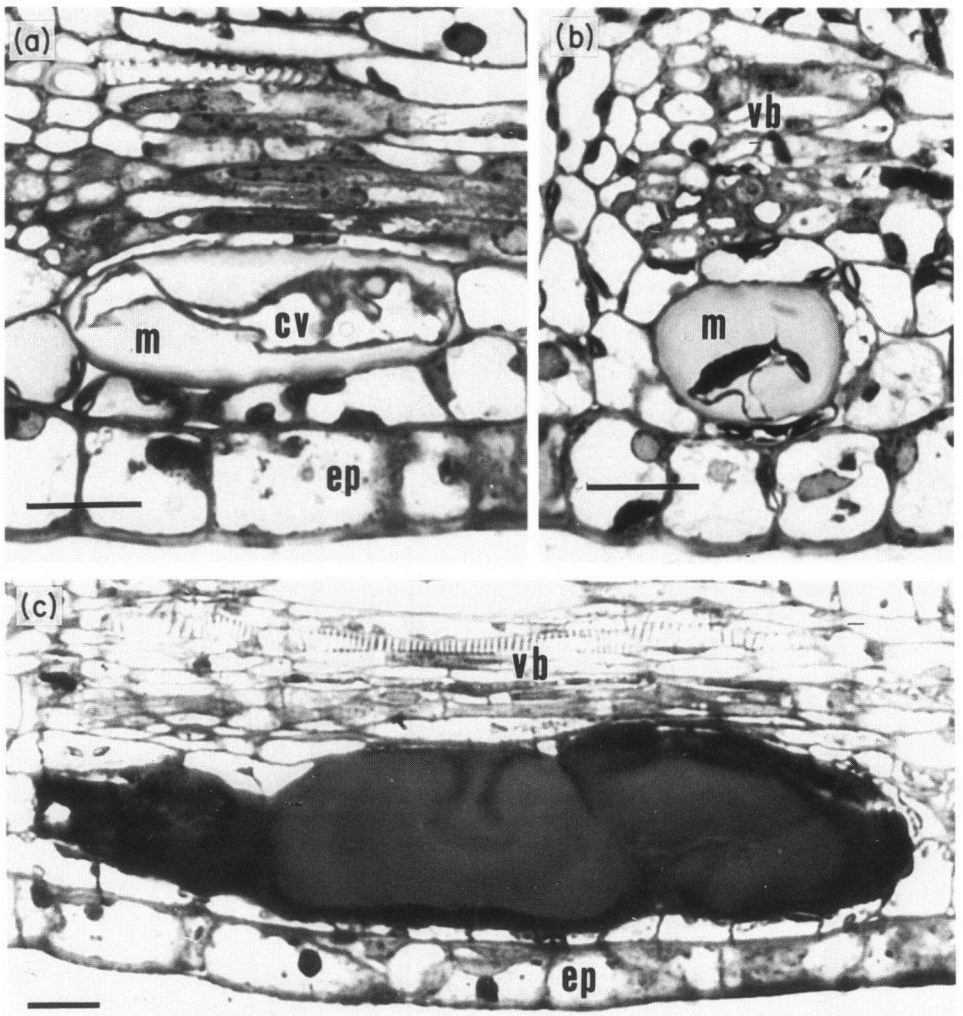

Fig. 2. *Hibiscus schizopetalus*. Light micrographs of the leaf. 1 μm transverse sections stained with toluidine blue O. (a) Longitudinally sectioned mucilage cell, underneath a minor vein. Note cytoplasmic strands surrounded by mucilage. The central vacuole is still present. Bar = 20 μm. (b) Detail of a cross-sectioned mucilage 'canal' underneath a minor vein. The central vacuole has disappeared; the cytoplasm is embedded in mucilage. Bar = 20 μm. (c) A large, mature mucilage canal cut longitudinally and located underneath a vascular bundle. Bar = 20 μm.

approximately 250 μm below the shoot apex in the peripheral ground tissue and in the undifferentiated mesophyll of the developing leaves. Mucilage was deposited as a thin layer between the cell wall and the plasma membrane (Fig. 1b). After prolonged mucilage deposition, the cytoplasm was present only in the central region of the cell, thereby surrounding a reduced central vacuole, which finally disappeared (Figs 1c, 2a and b). Eventually the whole cell lumen (area within the cell walls) was filled with mucilage (Figs 1d and e, 2c) in which only a few, thin degenerating cytoplasmic strands remained. No suberized layer could be recognized in the cell walls of these cells.

Local breakdown of the cell wall was often encountered, and by it mucilage 'canals' were formed. These 'canals' contained only mature mucilage cells (Figs 1e, 2c). The neighbouring non-mucilage cells then were intruded by mucilage.

Transmission electron microscopy. Very young (mucilage) cells in the apex were recognized by their size (29 μm × 18 μm) and the large central vacuole. The composition of the cytoplasm was identical to the adjacent cells except for the presence of typical plastids, which lacked well-defined thylakoids, and contained more distinct starch granules (Fig. 3a).

When mucilage was present between the cell wall and the plasma membrane three arbitrary developmental stages: a, b and c were distinguished.

Stage a. The mucilage cells (approximately 38 × 28 μm in size) appeared mostly in pairs. Some solitary cells and groups of four cells were also present. The mucilage was initially deposited as a thin layer between the cell wall and the plasma membrane (Fig. 3b). The central vacuole decreased in size as cytoplasm became more and more confined to the central region of the cell lumen, caused by the prolonged mucilage deposition. The nucleus was surrounded by typical plastids which lacked thylakoids and contained distinct starch granules (Fig. 3a). Many mitochondria and an abundance of hypertrophied dictyosomes, budding off vesicles, were present in the cytoplasm (Fig. 3a and b). Strands of rough endoplasmic reticulum (RER) were positioned parallel to the plasma membrane (Fig. 3a and b). Other RER strands surrounded organelles and small vacuoles. Ribosomes were either present as free ribosomes or grouped as polysomes. Small electron dense globules were present in the extraplasmatic space attached to the outer side of the plasma membrane (Fig. 3a and b).

Stage b. The mucilage cells in the shoot apex were approximately 63 × 25μm in size. Upon mucilage deposition, the cytoplasm was present in the centre of the cell at the cost of the central vacuole. The cytoplasm was filled with dictyosomes and vesicles, containing granular material resembling mucilage. The plastids could be recognized by their distinct starch granules. Local breakdown of the cell wall towards neighbouring non-mucilage cells was noticed many times. These intruded cells surrounded the mucilage cell as a kind of sheath. Breakdown of the cell wall between two adjacent mucilage cells also occurred.

Stage c. Large mature mucilage cells (up to 90 × 45 μm in size) showed (thin) strands of degenerating cytoplasm embedded in granular mucilage. Only remnants of dictyosomes, vesicles (Fig. 3c) and starch granules were recognized. A sheath of elongated small cells surrounded the mucilage cells and often contained degenerating cytoplasm and mucilage (Fig. 3d). The sheath cells apparently had been penetrated by mucilage originating from the large mucilage cells through local breakdown of the cell wall (arrow in Fig. 3d). The intact cell wall between two adjacent mucilage cells was very thin in the middle, only showing the more electron-dense middle lamella. Sometimes the common wall was broken and mucilage from a cell pair was continuous (Fig. 3c). Local cell-wall breakdown was also observed between mucilage cells of adjacent cell pairs. A suberized layer was never detected in the mucilage cells or the sheath cells.

Epidermal mucilage cells in the leaf

Light microscopy. Solitary epidermal mucilage cells appeared in the adaxial epidermis in relatively large numbers (approximately 1·5 mucilage cell/mm in mature leaves). The cells

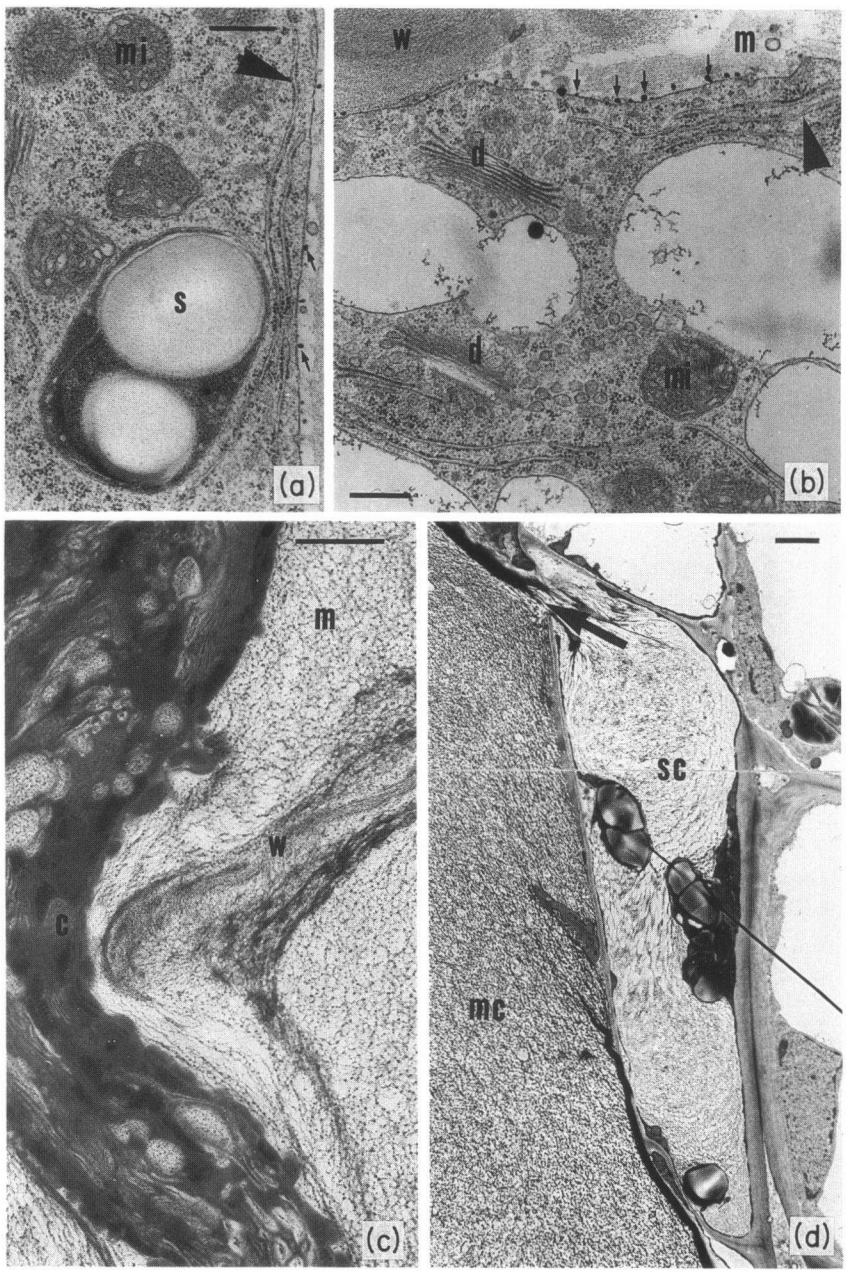

Fig. 3. *Hibiscus schizopetalus.* Transmission electron microscopy. Cytoplasmic details of mucilage cells in the shoot apex. a, b: Stage a. c, d: Stage c. (a) Plastid containing distinct starch granules, but lacking thylakoids. Note RER strands (arrowhead) and small electron dense globules (small arrows). Bar = 0·5 μm. (b) Detail showing dictyosomes, mitochondria, and strands of RER (arrowhead). Note small electron dense globules against the plasma membrane (small arrows). Bar = 0·5 μm. (c) Detail of the free end of a broken cell wall between two adjacent mucilage cells. The other free end of the broken cell wall is located in the area beyond the lower left part of this photograph. Note degenerated cytoplasm and surrounding mucilage flowing into the lower situated mucilage cell. Bar = 0·5 μm. (d) Detail of a sheath cell adjacent to a mucilage cell. Note local breakdown of the cell wall (arrow) through which mucilage has entered the sheath cell. Bar = 2 μm.

had a more or less conical shape with a blunt apex and protruded into the palisade parenchyma (Fig. 4b–f). The outer periclinal cell-wall appeared to be thickened (Fig. 4a–e), but the thickened part underneath the cuticle was not impregnated by cutin.

Very young epidermal (mucilage) cells (approximately 45 μm wide and 60 μm high) were a little larger in size than the adjacent epidermal cells. The cytoplasm, surrounding a large central vacuole, contained a nucleus, positioned near the inner periclinal wall (Fig. 4a). Mucilage was deposited as a thin layer between the inner periclinal cell-wall and the plasma membrane (Fig. 4b). When mucilage deposition continued the increased amount of mucilage caused the upward position of the cytoplasm (Fig. 4c). The central vacuole and the nucleus were still present. The cell width had increased to approximately 55 μm. In mucilage cells nearing maturity, the cytoplasm was confined to the adaxial part of the cell (Fig. 4d) and finally remained visible as a compressed degenerated cytoplasmic mass adjacent to the outer periclinal cell-wall (Fig. 4e). At maturity the epidermal mucilage cells had increased in size up to approximately 75 μm in width and 60 μm in height.

In thick sections of fresh leaf stained with alcian blue the mucilage showed a layered appearance (Fig. 4f). The cell size had increased by the swelling of the mucilage in the presence of water. No fluorescence of suberin was detected in the cell walls of these cells.

Transmission electron microscopy. Two young epidermal mucilage cells were studied with TEM. One very young cell, depicting the developmental stage as in Figure 4a, showed the distinctly thickened upper cell-wall (Fig. 5a). The parietal cytoplasm was identical to the adjacent epidermal cells except for the presence of typical plastids, which lacked a distinct thylakoid system.

Another mucilage cell appeared to be in the same developmental stage as depicted in Fig. 4b. This cell differed from the surrounding epidermal cells in size, shape and the presence of an extraplasmatic space. Further, a nucleus, plastids with starch granules and reduced thylakoids, mitochondria, RER strands and dictyosomes (Fig. 5b) were present. Many (small) electron-dense globules were present on the outside of the plasma membrane, in the cytoplasm and within the plastids (Fig. 5b). The extraplasmatic space in the lower region of the mucilage cell contained loosely arranged material, presumably mucilage (Fig. 5b).

DISCUSSION

The development of mucilage cells in *Hibiscus schizopetalus* in pairs (Fig. 1a–d) confirms the light microscopical observations of Dános and Juhász (1967).

Lysigenous mucilage cavities and canals have been described for the Malvales (Bouchet 1971, 1973; Bouchet & Deysson 1974, 1976; Nabeesa & Madhusudanan 1984) and some woody Ranales (West 1969). In the present study, the lysigenous origin was ascertained by the fact that the cell wall between two adjacent mucilage cells disintegrates and then breaks, presumably due to the pressure caused by the accumulating mucilage (Fig. 3c). The common presence of (small) lysigenous cavities or 'canals' is possibly related to the absence of a suberized layer in the cell wall. In *Cinnamomum* mucilage cells, which possess a suberized layer, single local breakdown of the cell wall was observed at low frequencies (Bakker *et al.* 1991).

The small 'canals' in shoot apices of *Hibiscus* resemble the mucilage canals of *Sterculia* (Bouchet & Deysson 1974). Both types of canals are surrounded by bordering cells. In *Hibiscus* we found sheath cells containing mucilage and degenerated cytoplasm (Fig. 3d),

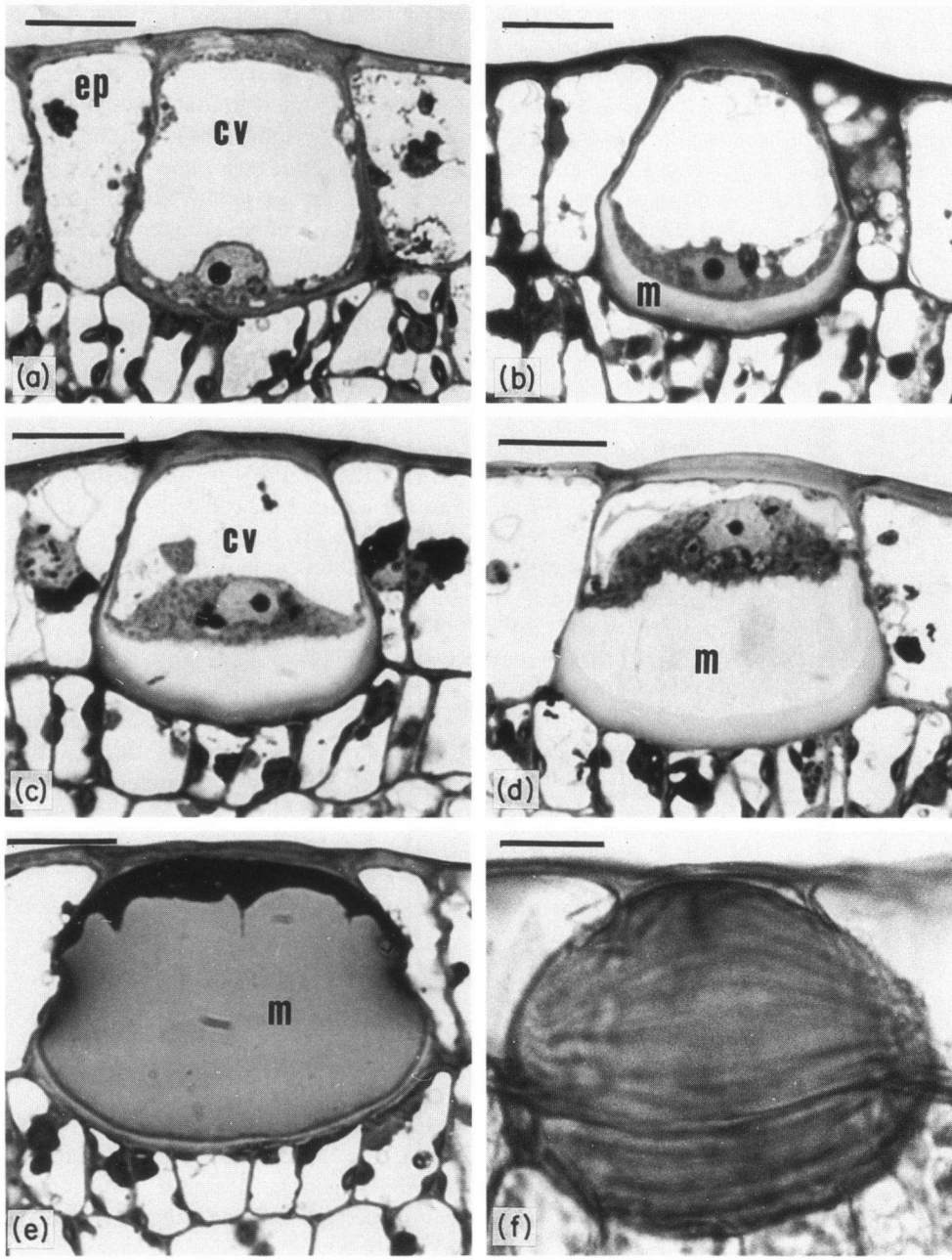

Fig. 4. *Hibiscus schizopetalus*. Light microscopy. Epidermal mucilage cells in the leaf. a–e: Developmental stages. 1 μm sections stained with toluidine blue. f; 30 μm section of fresh leaf, stained with alcian blue. (a) Very young stage with characteristically positioned nucleus at the bottom of the cell. Note the distinctly thickened upper cell wall. Bar = 20 μm. (b) Mucilage is deposited as a thin layer between the plasma membrane and inner periclinal cell wall. Bar = 20 μm. (c) After prolonged mucilage deposition cytoplasm is present in the upper half of the cell. Bar = 20 μm. (d) Near-mature mucilage cell. Note the disappearance of the central vacuole. The mass of deposited mucilage has accumulated. Bar = 20 μm. (e) Fully mature mucilage cell filled with densely stained mucilage. Degenerating cytoplasm is present against the outer periclinal cell-wall. Bar = 20 μm. (f) Mature epidermal mucilage cell in section of fresh material. Note layered appearance of mucilage. Bar = 20 μm.

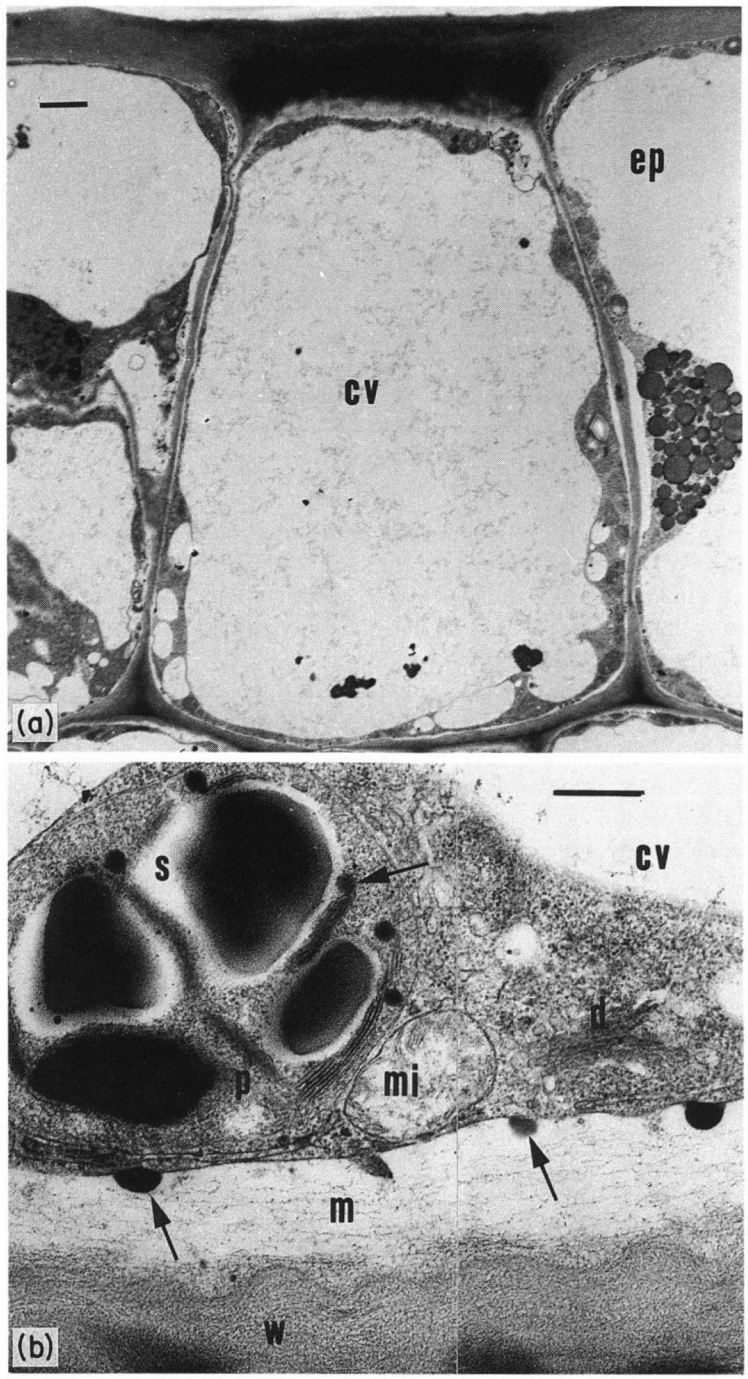

Fig. 5. *Hibiscus schizopetalus*. Transmission electron microscopy. Epidermal mucilage cells. a: Preceding mucilage deposition. b: Stage a. (a) Very young epidermal mucilage cell with characteristic conical shape and thickened upper cell-wall. Bar = 2 μm. (b) Detail of cytoplasm of epidermal mucilage cell, in stage a. Note plastid, containing starch granules, but lacking thylakoids; extraplasmatic mucilage; dictyosome and mitochondrion. Also, note small electron dense globules on the outer side of the plasma membrane and inside the plastid (arrows). Bar = 0·5 μm.

Table 1. Main differences and similarities in mucilage cell development between *Hibiscus* (Malvaceae) and *Cinnamomum* (Lauraceae) and *Annona* (Annonaceae)

	Hibiscus	*Cinnamomum* (*Annona*)
Suberized wall layer	−	+
Specific plastids in early developmental stage	+	+
High dictyosome activity	+	+
Cell-wall breakthrough	++	±
Mature organization	cavities/ canals	solitary cells

but these cells did not secrete mucilage. A possible function of the sheath cells in *Hibiscus* is the prevention of mucilage leaking into the surrounding tissue.

Walliczek (1893) reported the absence of plastids and starch in mucilage cells of the Malvaceae. In the mucilage cells of *H. schizopetalus* starch granules are, however, present and persist until cytoplasmic degeneration (Figs 3a and 5b). This is in agreement with the findings of Bouchet & Deysson (1976) that starch is not used for mucilage formation. In oil and mucilage cells of *Cinnamomum* (Bakker & Gerritsen 1989; Bakker *et al.* 1991) and in oil cells of *Annona* (Bakker & Gerritsen 1990) plastids, which lacked distinct thylakoids, were one of the first visible characteristics of future idioblasts. This feature is valid also for future mucilage cells in *Hibiscus*.

In the present study, mucilage cells were found in the adaxial epidermis only. This is in agreement with the light microscopical study of Rao & Ramayya (1984). While describing the distribution of the mucilage cells in leaves of Malvaceae Spegg (1959) did not report the presence of mucilage cells only in the adaxial epidermis (Fig. 4a–f).

In the epidermal mucilage cells of *H. schizopetalus*, the mucilage is deposited against the inner periclinal cell wall, without the deposition of a tertiary cellulose layer. This type was already described by Walliczek (1893).

Only a few ultrastructural reports on the development of epidermal mucilage cells are available. Yakovleva (1988) described the ultrastructural aspects of epidermal mucilage cells. Later she presented a figure of the development of epidermal mucilage cells (Yakovleva 1990: Fig. 1). The initial stages in the development of epidermal mucilage cells as described by Yakovleva (1990) resemble those reported for *Hibiscus* in the present study (Fig. 5a and b).

The development of mucilage cells in *Hibiscus schizopetalus* (excluding the epidermal mucilage cells) resembles that described for *Cinnamomum burmanni* (Bakker & Gerritsen 1989; Bakker *et al.* 1991). However, in mucilage cells of *Cinnamomum*, a suberized wall layer is deposited against the cell wall and remains present during further cell development. In *Hibiscus*, mucilage cells with no suberin were detected. The absence of suberin in the cell wall is in agreement with most (older) literature (reviewed by Gregory & Baas 1989), but is in contrast to a light microscopical report of a suberized layer in the mucilage cells in the fruits of *Hibiscus* (Scott & Bystrom 1970). The latter report is, however, not convincing due to the use of non-specific staining procedures.

Table 1 summarizes the main similarities and differences in mucilage cell development between *Hibiscus* and *Cinnamomum*.

The existence of mucilage cells with or without a suberized layer in the Dicotyledons, prompt us to consider the mucilage cells with a suberized wall layer as a type, separate from those described here, which presumably is typical of the Malvaceae. Families with the former type mostly possess both oil and mucilage cells (e.g. Lauraceae: Bakker & Gerritsen 1989; Bakker *et al.* 1991; and Annonaceae: unpublished results) which can be considered as homologous structures (Bakker *et al.* 1991). The presence of mucilage cells lacking a suberized wall layer in Malvaceae has been hypothesized as a synapomorphy for Malvales (Gregory & Baas 1989). Despite the different cell-wall composition, the similarities in development of both types of mucilage cells remain striking (Table 1). A phylogenetic relationship between the two types (as states of the same character) still is an intriguing possibility, which should be tested in future research.

ACKNOWLEDGEMENTS

The authors wish to thank Dr L. Goosen de Roo for critical reading of the manuscript and valuable advice, the curator of the Hortus Botanicus in Leiden for kindly providing fresh material of *Hibiscus schizopetalus* and M. Smits for her contribution to the TEM preparations. This work was supported by the Foundation for Fundamental Biological Research (BION), which is subsidized by The Netherlands Organization for Scientific Research NWO (grant no. 811-440-023, to M.E. Bakker).

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