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ULTRASTRUCTURAL STUDIES ON THE ONTOGENY OF GRAPEFRUIT JUICE VESICLES (CITRUS PARADISI MACF. CV STAR RUBY)[1]

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The ultrastructure of juice vesicle development and maturation was investigated in cv Star Ruby grapefruit. Juice vesicle primordia were initiated by divisions of epidermal and subepidermal cells on the adaxial surface of the carpel wall at least 2 d before anthesis. Development occurred in three distinct stages: cell division, cell elongation, and cell maturation. Development of juice vesicles in the first 3 wk postanthesis occurred by cell division of a subterminal meristem and resulted in the formation of a main juice vesicle body subtended by highly vacuolate stalk cells connected to the carpel wall. Cells of the main body were characteristic of meristematic cells. Between 4 and 10 wk postanthesis, oil gland/oil cavity development occurred in the center of the main juice vesicle body and began with a single electron-dense cell. Surrounding cells exhibited characteristics of intense metabolic and secretory activity, culminating in the synthesis of lipid and osmiophilic material. A schizogenous and/or lysigenous cavity developed in the central area of the main juice vesicle body, where fibrillar-oil material and lysed cell remnants were observed, respectively. Expansion of surrounding cells resulted in further lysigeny of the central electron-dense cells. The mature juice vesicle body contained highly vacuolate central cells surrounded by a hypodermis and epidermal layer. The central cavity remained even after 12 mo of juice vesicle development.

Introduction

Juice vesicle development, as in whole citrus fruit, can be divided into three distinct but overlapping stages: cell division, cell elongation, and cell maturation (Ford 1942; Bain 1958; Schneider 1968; Nii and Coombe 1988). The cell division stage is characterized by juice vesicle initiation at or before anthesis along the adaxial surface of the endocarp wall. Juice vesicles arise as a result of anticlinal and then periclinal divisions of epidermal and subepidermal cells of the endocarp. Cell divisions of a subterminal juice vesicle primordia meristem continue until the juice vesicles, with main body connected to the segment wall by a multicellular stalk, fill at least one-half of the segment space. The rate of cell division decreases as the cell enlargement phase commences, resulting in complete fill of the segment space. At the initiation of cell maturation, elongation ceases, soluble solids accumulate, and total acid declines. The entire juice vesicle is contained within an epidermis covered with a defined cuticle (Fahn et al. 1974; Espelie et al. 1980). Juice vesicles may contain a small lipid deposit within the main body at various stages of development.

Little chronological ultrastructural detail is available on the growth, development, and maturation of juice vesicles. In this report, we provide anatomical and ultrastructural detail with the use of light, scanning, and transmission electron microscopy on the initiation, growth, and maturation of grapefruit juice vesicles during 12 mo of development. In addition, we describe the development of the lipid deposit in the main body of the juice vesicle.

Material and methods

Plant material

Flowers, fruitlets, and fruit of cv Star Ruby grapefruit (*Citrus paradisi* Macf.) were collected from a single tree at the Citrus Arboretum, Florida Department of Agriculture, Winter Haven. In February 1990, at least six flower buds were collected 2 d prior to and at anthesis. Additional flowers were tagged at anthesis, and at least six fruitlets or fruits were collected at various times postanthesis for up to 12 mo. Organs were brought to the laboratory and weighed, and measurements of distance were taken from stem to stylar end and of the equatorial diameter. Whole ovaries or fruitlets were utilized for microscope studies for the first 28 d of development, after which individual juice vesicles were excised and utilized for further study.

Scanning electron microscopy

Whole ovaries and fruitlets were observed with the scanning electron microscope. Using a razor blade, longitudinal sections were made through the organs. The tissue was fixed in 3% glutaraldehyde in 0.2 M K_2HPO_4 (pH 7.0) for 3–4 h at ambient temperature, followed by postfixation in buffered 2% OsO_4 for 2 h as described by Burns and Achor (1989). After dehydration in an ethanol series, the tissue was critical point dried, sputter-coated with gold, and viewed with a Hi-

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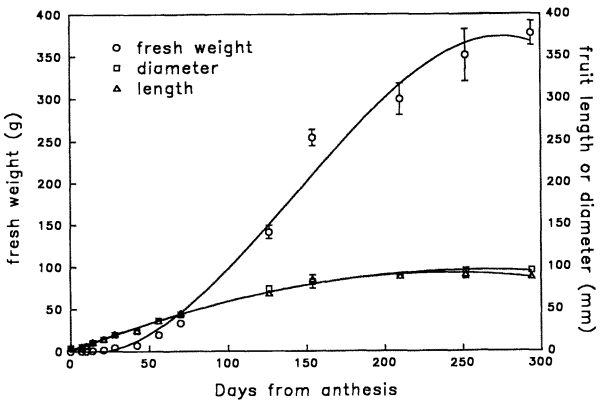

Fig. 1 Fruit fresh weight, length, and diameter of cv Star Ruby grapefruit from anthesis to 300 d of fruit development. Data plotted are the means of at least six fruitlets or fruit, with error bars indicating standard deviation.

tachi S530 scanning electron microscope at 20 kV.

Light and transmission electron microscopy

Whole ovaries, fruitlets, and juice vesicles were used for light microscopy and transmission electron microscopy. Longitudinal or cross-sections were made with a razor blade through young ovaries or fruitlets, and fixation and postfixation were performed as described above. In some cases, especially later in fruit development, longitudinal and cross-sections were made through intact juice vesicles after fixation but before postfixation. After dehydration in an ethanol series, the tissue was polymerized in L. R. White or Spurr's resin (Spurr 1969) overnight at 60 C or at 70 C for 24 h, respectively. Thick sections (1 μm) were cut with a microtome and stained with methylene blue-azure A/basic fuchsin. The sections were mounted and viewed with an Olympus BH-2 light microscope. Thin sections (0.1 μm) were cut and stained with 4% aqueous or methanolic uranyl acetate for 15 min and poststained with 0.5% lead citrate for 5 min (Stempak and Ward 1964). The sections were then viewed with a Philips 201 transmission electron microscope at 60 kV.

Results

Fruit growth

Fresh weight of grapefruit fruit followed a typical sigmoidal growth curve during the 300 d of study (fig. 1). Three growth stages could be distinguished in fruit of Star Ruby grapefruit. Stages 1, 2, and 3 were approximately 8 wk, 10–22 wk, and equal to or greater than 23 wk postanthesis, respectively. Trends in fruit length and diameter were similar throughout the sampling period. Both length and diameter increased in a linear fashion for the first 150 d postanthesis, after which no further increases were measured.

Juice vesicle initiation and early growth

Juice vesicles initially appeared as small elevated areas and were initiated at least 2 d prior to anthesis along the adaxial surface of the carpel wall (figs. 2, 3). Juice vesicles originated from divisions of epidermal and subepidermal cells (fig. 4). The meristematic cells were densely cytoplasmic and, in contrast to cells of the ovary wall, lacked well-formed, large central vacuoles. Juice vesicle primordia continued to increase in size (fig. 5), and divisions continued to occur 3 d postanthesis in the juice vesicle initials (figs. 6, 7). By 10 d postanthesis, highly vacuolated stalk cells were differentiated and subtended the meristematic region of the juice vesicle (figs. 8–10). As divisions continued, carpellary outgrowths and developing juice vesicles, each distinctly different, were scattered throughout the surface of the carpel wall (figs. 6, 8). Carpellary outgrowths, visible 3 d after full bloom (figs. 5, 6), had a well-defined stalk region after 10 d postanthesis (fig. 9). The terminal region of the carpellary outgrowth contained greatly enlarged cells which continued to divide. Intercellular spaces of the carpellary outgrowths were also filled on occasion with darkly staining material, apparently produced by the large globose cells.

Juice vesicles continued to elongate and fill the segment space after 3 wk postanthesis (fig. 11). Carpellary outgrowths remained a prominent feature. Light and transmission electron micrographs revealed that stalk cells continued to differentiate, while the main body of the juice vesicle remained meristematic (figs. 12, 13). Meriste-

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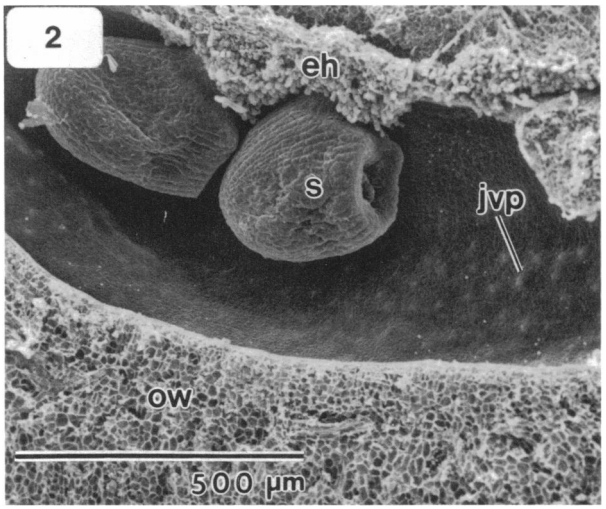
Figs. 2–7 Juice vesicle development 2 d before and 3 d after anthesis in grapefruit. Fig. 2, Scanning electron micrograph of juice vesicle initiation along the carpel wall 2 d prior to anthesis, in longitudinal section. Fig. 3, Light micrograph of juice vesicle initiation 2 d before anthesis. Fig. 4, Transmission electron micrograph of a juice vesicle primordium 2 d before anthesis. Fig. 5, Scanning micrograph of juice vesicles and carpellary outgrowths 3 d postanthesis. Fig. 6, Light micrograph of juice vesicles and carpellary outgrowths 3 d postanthesis. Fig. 7, Transmission micrograph of juice vesicle 3 d postanthesis. *ce,* carpel epidermis; *co,* carpellary outgrowth; *eh,* epidermal hairs; *jvp,* juice vesicle primordium; *ow,* ovary wall; *s,* seed; *vt,* vascular tissue.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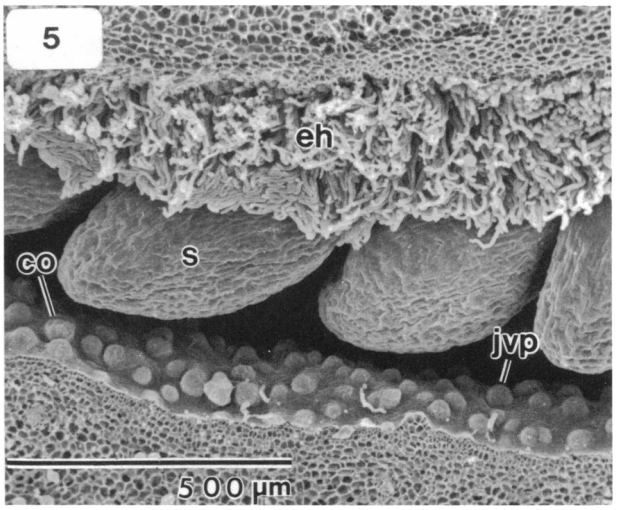
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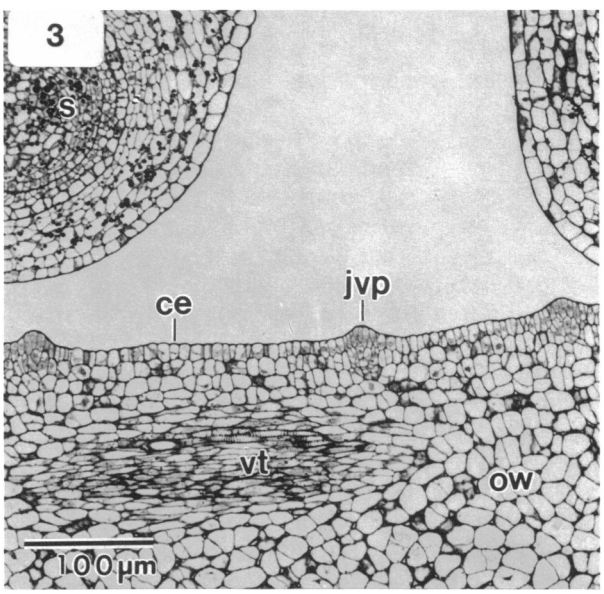
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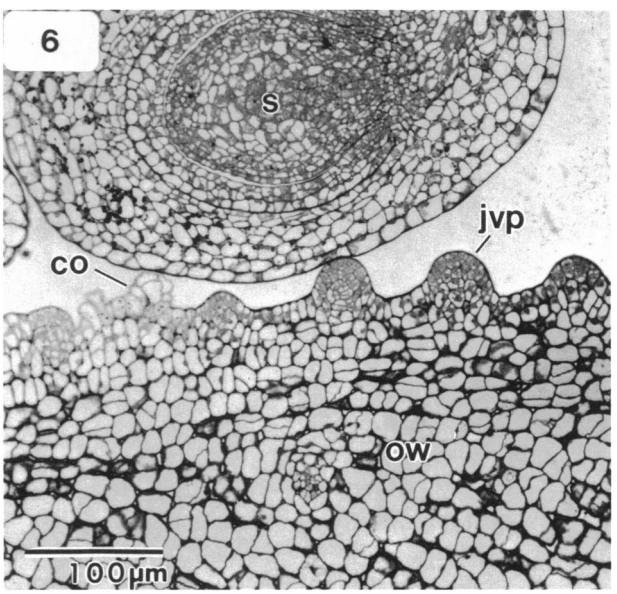
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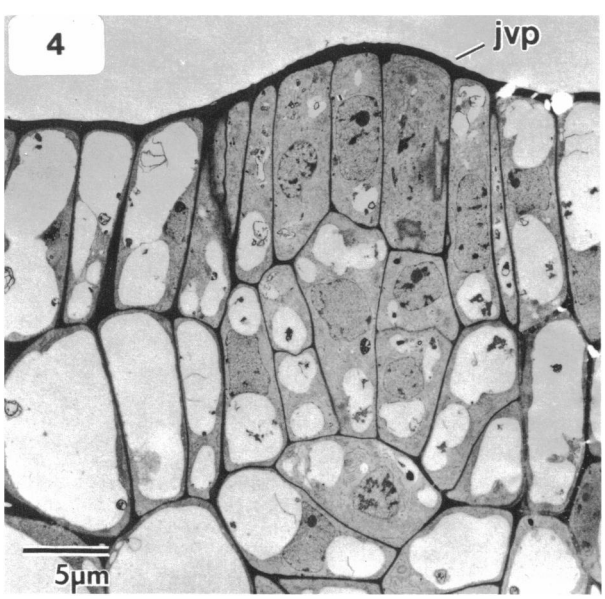
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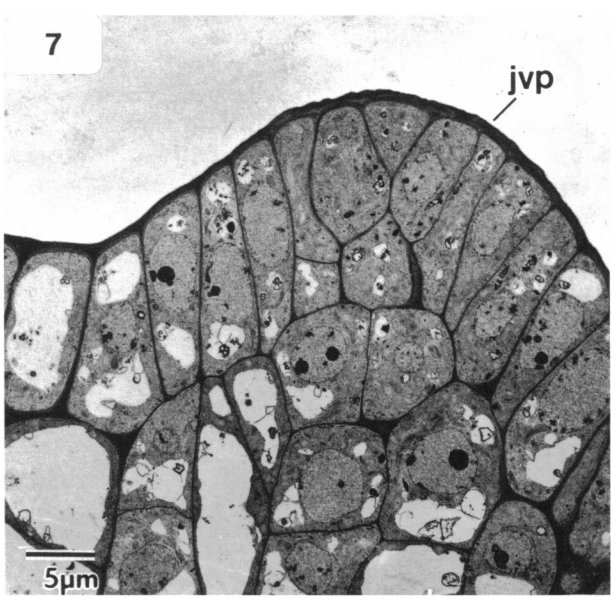
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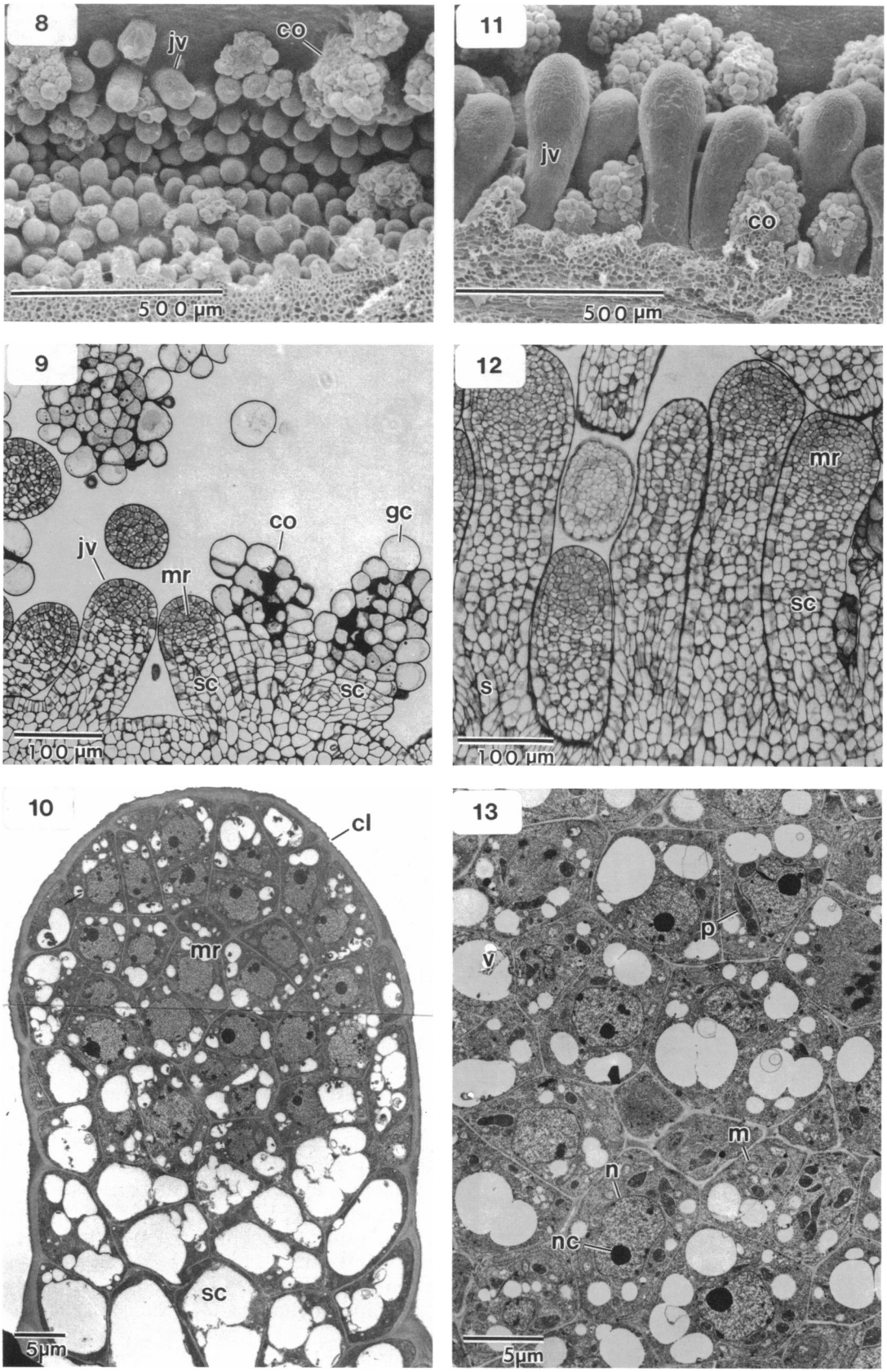
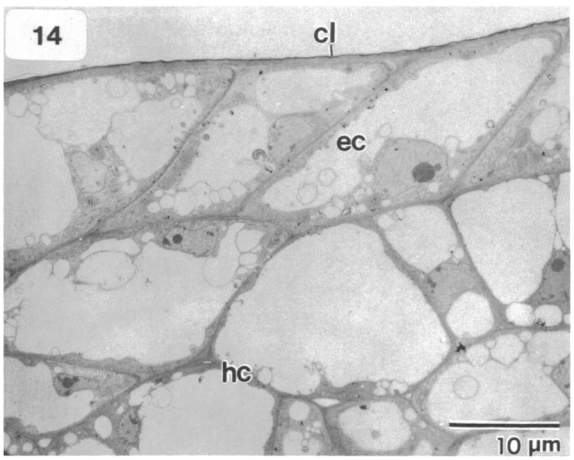
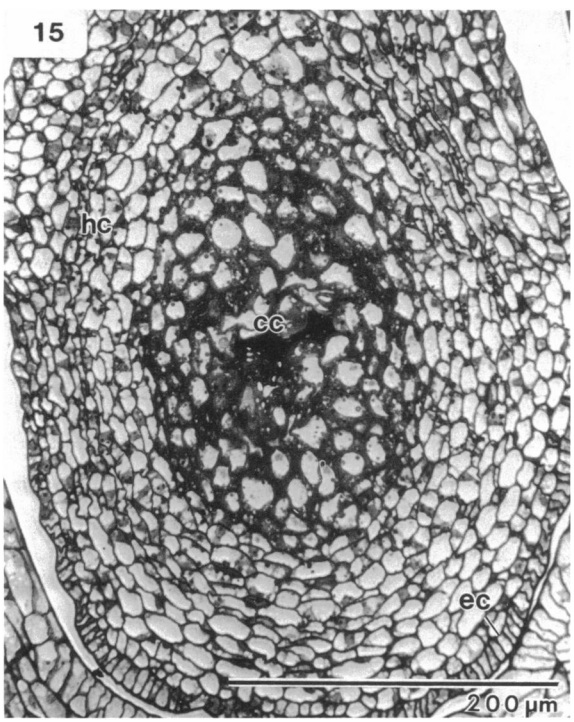
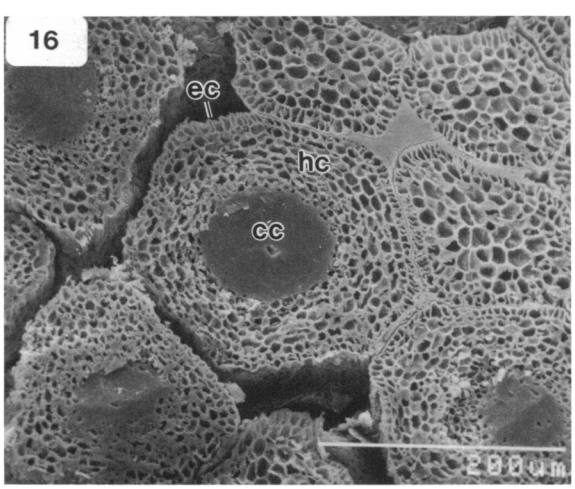


Figs. 8–13 Juice vesicle development 10 and 21 d postanthesis. Fig. 8, Scanning micrograph of juice vesicles and carpellary outgrowths 10 d after anthesis. Fig. 9, Light micrograph of juice vesicles and carpellary outgrowths 10 d postanthesis. Fig. 10, Transmission micrograph of a developing juice vesicle 10 d postanthesis. Fig. 11, Scanning micrograph of juice vesicles and carpellary outgrowths 21 d postanthesis. Fig. 12, Light micrograph of developing juice vesicles 21 d postanthesis. Fig. 13, Transmission micrograph of the meristematic region in the developing juice vesicle main body 21 d postanthesis. *cl*, cuticular layer; *co*, carpellary outgrowth; *gc*, globose cell; *jv*, juice vesicle; *m*, mitochondria; *mr*, meristematic region; *n*, nucleus; *nc*, nucleolus; *p*, plastid; *sc*, stalk cells; *v*, vacuole.







matic cells continued to divide and were observed to contain well-formed nuclei with nucleoli, abundant mitochondria, small but numerous vacuoles, plastids, and endoplasmic reticulum (ER) (fig. 13).

Central cavity development

After 4–10 wk of development, a defined epidermal layer with surface cuticular material encircled the juice vesicle (figs. 14, 15). Directly beneath, a distinct 3–8 cell layer hypodermis developed. At this time, both epidermis and hypodermis were either highly vacuolate or becoming so, with smaller vacuoles coalescing to form larger ones. The peripheral cytoplasm contained mitochondria, nuclei, Golgi, rough and smooth ER, and plastids. Occasionally, the plastids in these two cell layers contained starch grains.

The central portion of the main juice vesicle body remained densely cytoplasmic. Often, an intensely stained multicellular area, defined as the central cavity, was detected in the center of the juice vesicle (fig. 15). When viewed with the scanning electron microscope, cross-sections made by hand through vesicles of this age revealed a striking contrast between the dense central cavity of the juice vesicle and the vacuolated cells of the encircling tissue (fig. 16).

A distinct transition zone was observed between the hypodermal and central regions of the juice vesicle. The cytoplasm of cells in this transition area exhibited a gradual increase in electron density as the cells were positioned closer to the center of the juice vesicle (figs. 17, 18). As the cytoplasm became increasingly electron dense, starch grains became more abundant within the plastids. The plastids also became increasingly reticulate (fig. 19) and contained numerous small lipid-like inclusions and plastoglobuli (figs. 17–21). Numerous lipid bodies of various sizes were scattered throughout the cytoplasm. In some cells, lipid bodies appeared partially digested, sometimes leaving apparent devoid areas (figs. 18, 20). Frequently, lipid bodies appeared to be engulfed by the large, developing central vacuole (fig. 20). Mitochondria were also abundant in these transition cells. Black, osmiophilic material was seen in close association with the periplasmic space of these cells (fig. 20). Before periplasmic deposition, osmiophilic material was frequently observed within plastids (fig. 21), in close association with ER (figs. 19, 21, 22), and finally with plasmodesmata (fig. 22). Dilated ER elements

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Figs. 14–16 Central cavity development in juice vesicles 4–10 wk postanthesis. Fig. 14, Transmission micrograph of epidermal and hypodermal areas of a typical juice vesicle 4–10 wk postanthesis. Fig. 15, Light micrograph of the juice vesicle main body showing development of the central cavity. Fig. 16, Scanning micrograph of several juice vesicles showing the presence of the central cavity. *cc,* central cavity; *cl,* cuticular layer; *ec,* epidermal cells; *hc,* hypodermal cells.

were often seen. Association of the osmiophilic material with multivesicular bodies was also observed (fig. 19). No association of the osmiophilic material with Golgi was seen.

Two significant events were observed to occur at or near the juice vesicle center at 4–10 wk postanthesis. Bulbous pockets began to form between the walls of electron-dense cells (fig. 23). Less electron-dense cells close to areas with bulbous pocket formation contained numerous mitochondria (fig. 23), and their plastids were filled with starch grains. The cytoplasm of dense cells was filled with plastids which contained osmiophilic material and large, free cytoplasmic osmiophilic droplets apparently independent of plastids. Starch grains were not as numerous in plastids of very electron-dense cells at or near the juice vesicle center. Larger pockets were also observed, with smaller pockets developing in close proximity (figs. 24, 25). Large pockets contained fibrillar material, and occasionally oil droplets were seen. In addition to this apparent schizogenous development of a central cavity, lysigenous development was also observed. The cytoplasm of electron-dense cells in the central region, filled with numerous lipid droplets, mitochondria, and plastids, began also to accumulate fibrillar material (figs. 26, 27). An increase in periplasmic space was seen in this area (fig. 27). Further sectioning in this area revealed a central cavity filled with cytoplasmic remnants of trapped cellular organelles and collapsed cell walls (fig. 28), indicating that this area had developed by lysigeny.

Cell enlargement and maturation

Epidermal, hypodermal, and central cells began to enlarge by 10 wk of juice vesicle development (fig. 29). Further cell divisions were only observed in epidermal cells occasionally between 10 and 22 wk of development. Epidermal and hypodermal cells had become highly vacuolate, often with fibrillar material contained within the vacuole. Central parenchyma cells rapidly increased in size, and the vacuole occupied most of the cellular volume (fig. 30). A thin parietal layer of cytoplasm was also present.

The central cavity was persistent throughout this developmental period (figs. 31, 32). As cells surrounding the central cavity continued to enlarge, central cells with electron-dense cytoplasm began to lyse and collapse, adding fibrillar material, lipid, and cell wall to the central cavity (fig. 33). Further development of large pockets that formed during the cell division stage was not observed, indicating that oil gland development was arrested.

After 22 wk of juice vesicle development, no changes in ultrastructure were evident in either the epidermis, hypodermis, or central cells. As the central cells continued to enlarge, the central cavity became less apparent but, nevertheless, persisted even after 12 mo of juice vesicle development (fig. 34). Contents of the central cavity appeared compressed, and remnants of cell wall, lipid/osmiophilic material, and fibrillar material were observed (fig. 35).

Discussion

In the grapefruit variety Star Ruby, juice vesicles were initiated at least 2 d prior to anthesis along the adaxial surface of the carpel wall. Prebloom initiation has been reported in satsuma mandarin (Nii and Coombe 1988) and cv Eureka lemon (Ford 1942). Juice vesicle initiation at anthesis has also been reported (Banerji 1954; Bain 1958; Schneider 1968).

Juice vesicles of Star Ruby grapefruit arise from divisions of the epidermal and subepidermal cells of the carpel wall. The results of this study strongly agree with previous reports on the initiation and growth of citrus juice vesicles during the first 4 wk after anthesis (Ford 1942; Banerji 1954; Bain 1958; Schneider 1968; Nii and Coombe 1988, 1990). Briefly, continued divisions of the primordium after 7–10 d of development give rise to a juice vesicle with a highly vacuolated, multicellular stalk, above which occurs a subterminal meristem and an epidermal layer. The ultrastructure of the cells of the main juice vesicle body is that characteristic of meristematic cells.

Carpellary outgrowth initiation began approximately 3 d postanthesis, and cells were distinct in appearance. Further growth resulted in the development of a stalk that terminated in numerous large globose cells which, during the early growth stages, surpassed the juice vesicles in size. The function of the carpellary outgrowth is unknown; however, Schneider (1968) suggested that these structures were responsible for the secretion of

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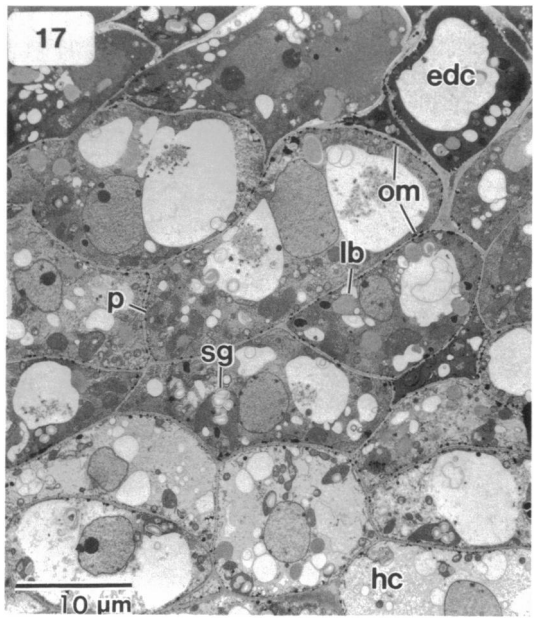
Figs. 17–22 Transmission electron micrographs of central cavity ultrastructure in juice vesicles 4–10 wk postanthesis. Fig. 17, Gradation of cellular electron densities in the transition area of the central cavity. Fig. 18, Central electron-dense cell surrounded by secretory cells. Fig. 19, Reticulate plastid with multivesicular bodies and endoplasmic reticulum in close association with osmiophilic material. Fig. 20, Secretory cells showing engulfment of lipid by vacuoles and osmiophilic material in association with periplasmic space. Fig. 21, Plastid with, and endoplasmic reticulum in association with, osmiophilic material. Fig. 22, Free cytoplasmic osmiophilic material and in association with multivesicular bodies, endoplasmic reticulum, and plasmodesmata. *edc,* electron-dense cell; *er,* endoplasmic reticulum; *hc,* hypodermal cell; *lb,* lipid body; *m,* mitochondria; *mvb,* multivesicular body; *om,* osmiophilic material; *p,* plastid; *pd,* plasmodesmata; *pg,* plastoglobuli; *rp,* reticulate plastid; *sg,* starch grains; *v,* vacuole.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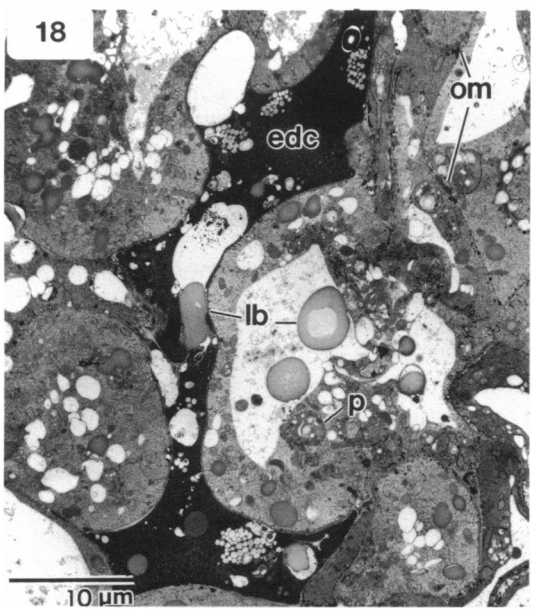
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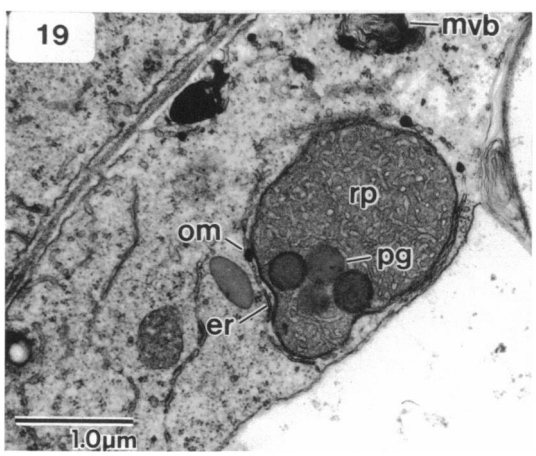
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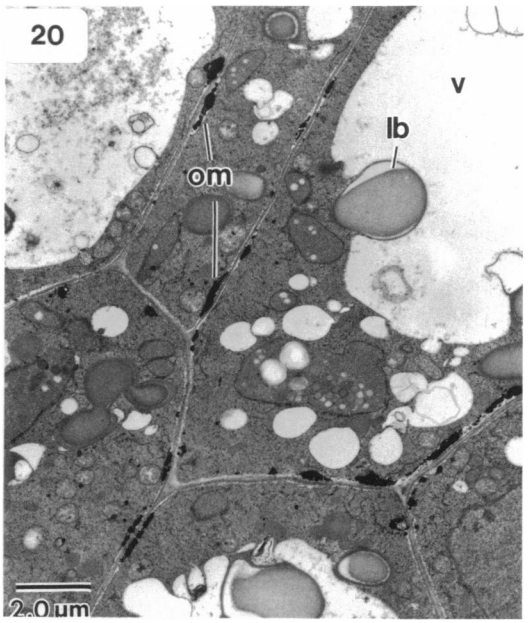
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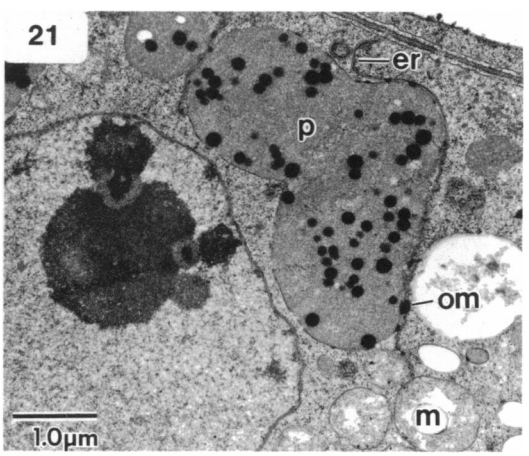
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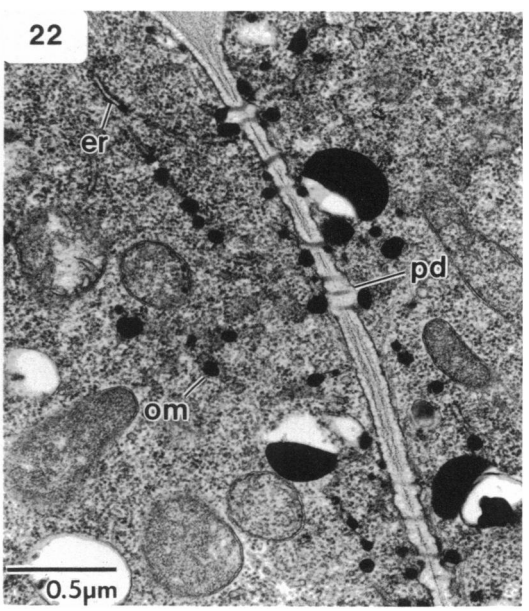
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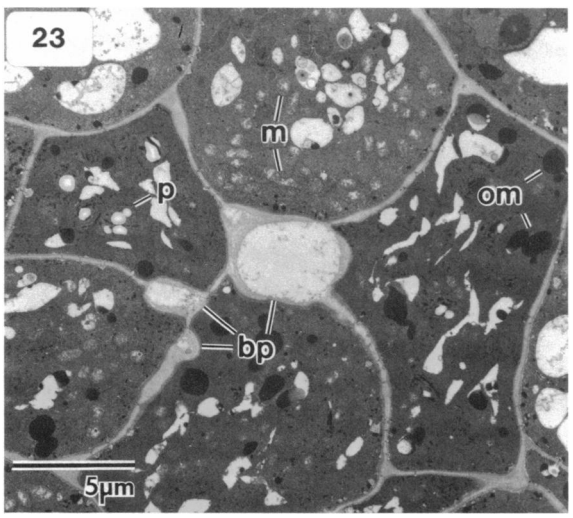
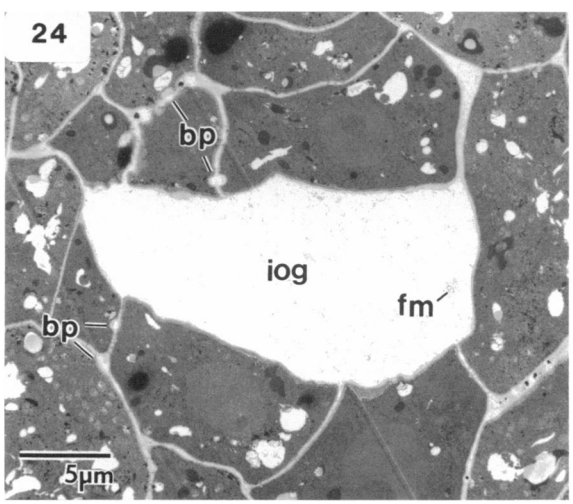
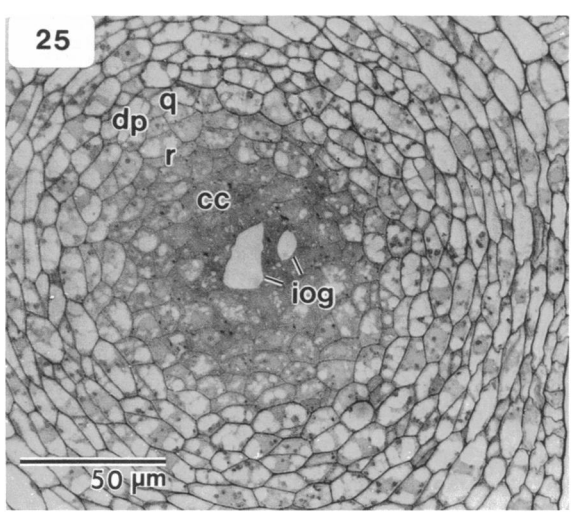




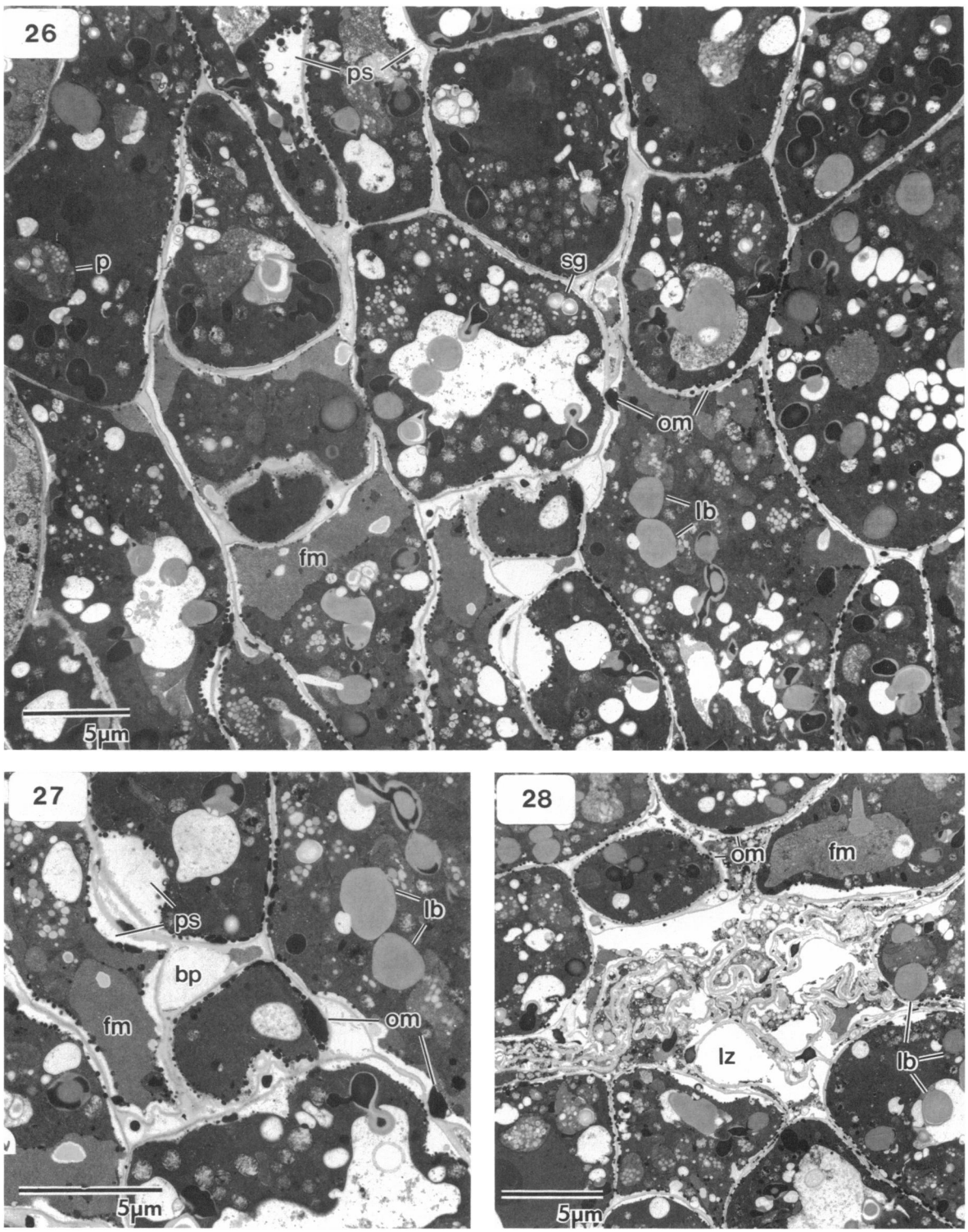


Figs. 23–25 Schizogenous and lysigenous development of the juice vesicle central cavity 4–10 wk postanthesis. Fig. 23, Transmission micrograph of bulbous pocket formation near the central electron-dense cells of the developing cavity. Fig. 24, Transmission micrograph of large pocket formation in the juice vesicle central cavity. Fig. 25, Light micrograph of an apparent immature oil gland in the juice vesicle central region. *bp,* bulbous pockets; *cc,* central cavity; *dp,* developing internal parenchyma; *fm,* fibrillar material; *iog,* immature oil gland; *m,* mitochondria; *om,* osmiophilic material.

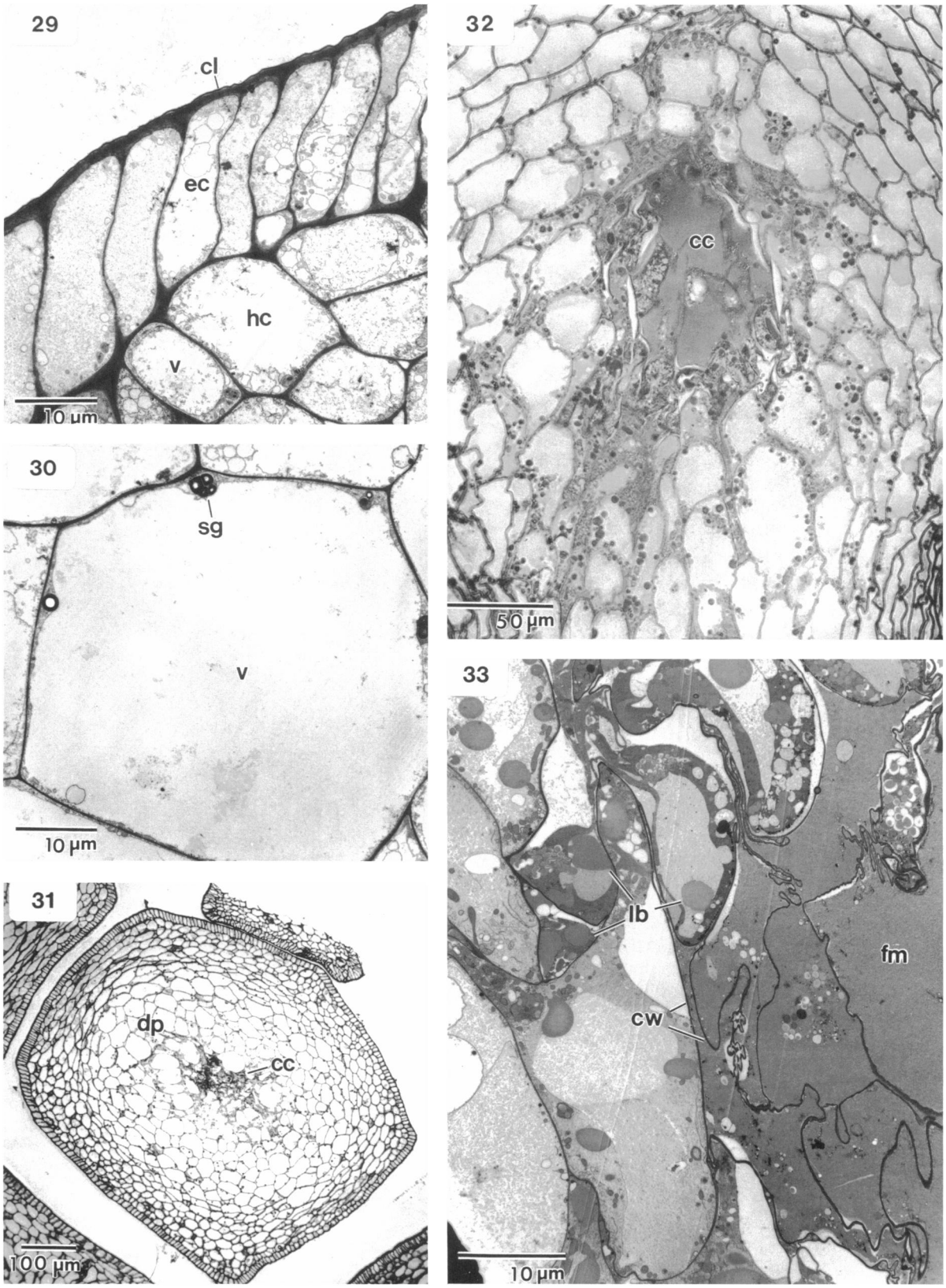
the gelatinous material prevalent in the segment space early in fruit development. Ford (1942) found no evidence of any secretory product from the carpellary outgrowth in lemon. Light micrographs of the outgrowths in Star Ruby grapefruit indicate that the large globose cells of the outgrowth terminus may secrete a dark-stained material which is present in the intercellular spaces. Whether this material was actually secreted into the segment space was not determined. The ultrastructure and possible function of the carpellary outgrowth are currently under investigation.

Oil deposits in the juice vesicles of citrus were reported by Davis (1932) and Dodd (1944), where observations were made with hand sections and histochemical staining techniques. Over 60 different *Citrus* species were surveyed that contained the oil deposit (Davis 1932). Further anatomical description of the oil droplet area has not been pursued. Our results indicate that the oil droplet area develops in the juice vesicle center between 4 and 10 wk after anthesis and is distinct from the subterminal meristem.

The ultrastructure of the development of the oil droplet area in juice vesicles of Star Ruby grapefruit is strikingly similar to oil gland development in the pericarp (flavedo) of *Citrus deliciosa* and leaves of *Citrus sinensis* (Thomson et al. 1976; Bosabalidis and Tsekos 1982*a,* 1982*b*). That we have used very similar fixation and staining techniques lends credibility to the comparisons. The opening of the juice vesicle central space began with a central cell of high electron density. The cells immediately surrounding this central cell accumulated copious amounts of free cytoplasmic and plastid lipid which, in the free lipid, were in various stages of digestion. Lipid bodies, presumably originating from plastoglobuli in the plastids, were also frequently engulfed by vacuoles, but definitive evidence of engulfment by the use of serial sections was not obtained. Although significant amounts of lipid-like bodies were observed in the central area, the lipid did not exclusively fill either the bulbous pockets or the central cavity. It is interesting that marked acid accumulation occurs during this time (Hirai and Ueno 1977), which suggests that lipid could be utilized as a carbon source for citrate synthesis. This same lipid accumulation, partial digestion, and apparent engulfment by vacuoles was observed in the ultrastructural development of the immature oil gland in citrus leaves (Thomson et al. 1976). Since the cytoplasmic lipid was ultrastructurally dissimilar to the lipid ultimately found in the oil gland, it was postulated that the lipid



Figs. 26–28 Schizogenous and lysigenous development of the juice vesicle central cavity 4–10 wk postanthesis. Figs. 26–27, Transmission micrographs of the juice vesicle central area showing osmiophilic material accumulation and dilation of the periplasmic space. Fig. 28, Transmission micrograph of lysigenous cavity development in the juice vesicle central region. *bp,* bulbous pockets; *fm,* fibrillar material; *lb,* lipid body; *lz,* lysigenous zone; *om,* osmiophilic material; *p,* plastid; *ps,* periplasmic space; *sg,* starch grains.



Figs. 29–33 Light and transmission electron microscopy of cell enlargement of developing juice vesicles between 11 and 22 wk postanthesis. Fig. 29, Transmission micrograph of the epidermal and hypodermal layers of a typical juice vesicle. Fig. 30, Transmission electron micrograph of an internal parenchyma cell of an enlarging juice vesicle. Fig. 31, Light micrograph of a juice vesicle in cross-section. Fig. 32, Light micrograph of the central cavity of an enlarging juice vesicle. Fig. 33, Transmission micrograph of the central cavity in an enlarging juice vesicle. *cc,* central cavity; *cl,* cuticular layer; *cw,* cell wall; *dp,* developing internal parenchyma; *ec,* epidermal cells; *fm,* fibrillar material; *hc,* hypodermal cells; *lb,* lipid body; *sg,* starch grains; *v,* vacuole.

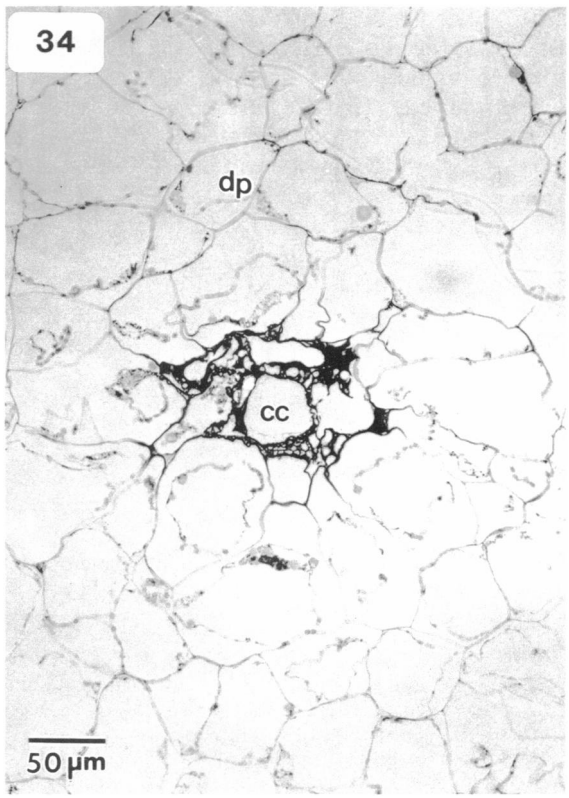
was utilized as a precursor for essential oils present in the gland itself.

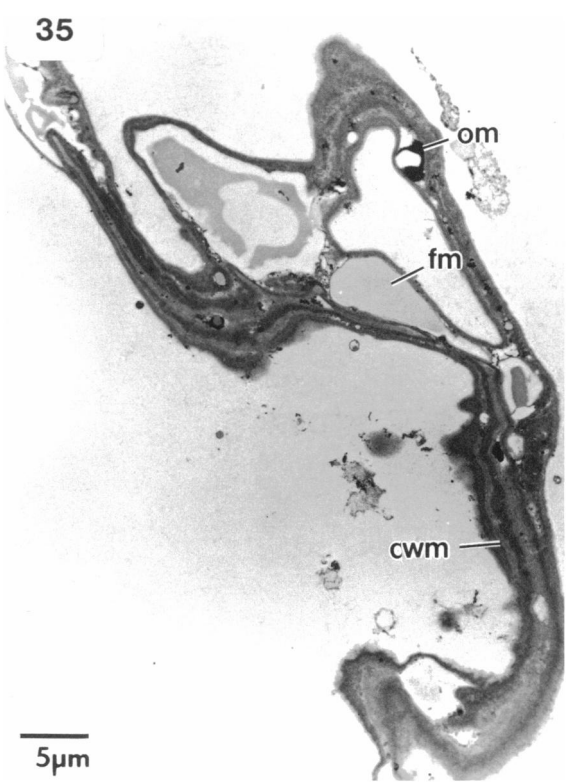
Concomitant with the development of electron-dense cells and the presence of lipid bodies was the deposition of osmiophilic material in the periplasmic space of central cells. Osmiophilic material, apparently synthesized in the plastids, was found in close association with ER which was near the plastids. Similar ER-plastid-osmiophilic material association was also found in *C. deliciosa* (Bosabalidis and Tsekos 1982*b*). Transportation of the material to the cell wall area occurred via the ER, and aggregation was confluent with the plasmodesmata, where finally the material was deposited into the periplasmic space. The identity of the osmiophilic material is unknown, but similar materials have appeared in secretory structures of citrus and have been referred to as lipophilic in nature (Thomson et al. 1976; Bosabalidis and Tsekos 1982*b*). Alternatively, the osmiophilic material could be a phenolic or tannic substance such as that found in certain phenolic-storing cells (Mueller and Beckman 1976).

The chronological sequence of events culminating in the development of the central cavity remains uncertain. However, we surmise that the opening of the central cavity begins with the development of a central electron-dense cell(s). Surrounding cells begin a period of intense metabolic activity, characterized by synthesis of lipid and starch, formation of many small vacuoles, and appearance of periplasmic osmiophilic material. Several electron-dense cells may develop, and, in this area, schizogenous separation of the cell wall occurs and bulbous pockets begin to form. Separation of the cell walls may result in the formation of a central large oil-like gland that may fill with fibrillar material and partially with oil. In juice vesicles where bulbous pockets occurred, no clear development of a ring of surrounding cells with thickened cell walls was observed, as was reported with oil gland development in citrus leaves and citrus pericarp (Thomson et al. 1976; Bosabalidis and Tsekos 1982*b*).

Further development of an organized oil gland appeared to be arrested, and electron-dense cells surrounding the gland underwent lysis. The cells undergoing lysis were characterized by the appearance of large amounts of osmiophilic material and extreme dilation of the periplasmic space. The sequestration of the osmiophilic material by plastids and ER sheds some degree of doubt on the role of cellular toxicity as a cause of lysis. Even so, the tendency of the material to accumulate at the plasmodesmata could possibly prevent cell to cell communication and result in the eventual death of the cells.

As cells exterior to the central cavity area undergo expansion, lytic cells may become crushed.





Figs. 34–35 Central cavity of a mature, 12-mo postanthesis, juice vesicle. Fig. 34, Light micrograph of the central cavity. Fig. 35, Transmission micrograph of the central cavity showing cell wall, osmiophilic material, and fibrillar material. *cc,* central cavity; *cwm,* cell wall material; *dp,* developing internal parenchyma; *fm,* fibrillar material; *om,* osmiophilic material.

Thus, the central cavity often contains remnants of cell wall, lipid bodies, osmiophilic and fibrillar material, and plastids. Indeed, after 12 mo of development, a very small translucent, often linear area can frequently be seen with the unaided eye in most all main juice vesicle bodies. The presence of lipid, osmiophilic material, and cell wall remnants in this translucent area of very mature juice vesicles suggests that the translucent area is a remainder of the central cavity once formed early in juice vesicle development.

Oil glands in *Citrus* leaves and pericarp are originally derived from subepidermal cells (Thomson et al. 1976; Bosabalidis and Tsekos 1982*a*). In leaves, the gland is initiated on both the abaxial and adaxial surfaces, whereas in the carpel, oil glands have been described only on the abaxial surface (the pericarp or flavedo). Juice vesicles are derived from epidermal and subepidermal cells of the adaxial surface of the carpel, itself a modified leaf. Discussions in the literature (e.g., Ford 1942) about the possible origins of juice vesicles argue against the derivation from oil glands themselves. The results of our study neither confirm nor deny such derivations but do indicate that the genetic message for oil gland/oil cavity development is present and expressed in the developing juice vesicle.

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