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ULTRASTRUCTURAL DEVELOPMENT OF CAPITATE GLANDULAR HAIRS OF CANNABIS SATIVA L. (CANNABACEAE)[1]

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ABSTRACT

The capitate-sessile and capitate-stalked glands of the glandular secretory system in *Cannabis*, which are interpreted as lipophilic type glandular hairs, were studied from floral bracts of pistillate plants. These glands develop a flattened multicellular disc of secretory cells, which with the extruded secretory product forms the gland head and the auxiliary cells which support the gland head. The secretory product accumulates beneath a sheath derived from separation of the outer wall surface of the cellular disc. The ultrastructure of secretory cells in pre-secretory stages is characterized by a dense ground plasm, transitory lipid bodies and fibrillar material, and well developed endoplasmic reticulum. Dictyosomes and dictyosome-derived secretory vesicles are present, but never abundant. Secretory stages of gland development are characterized by abundant mitochondria and leucoplasts and by a large vacuolar system. Production of the secretory product is associated with plastids which increase in number and structural complexity. The plastids develop a paracrystalline body which nearly fills the mature plastid. Material interpreted as a secretion appears at the surface of plastids, migrates, and accumulates along the cell surface adjoining the secretory cavity. Extrusion of the material into the secretory cavity occurs directly through the plasma membrane–cell wall barrier.

THE GLANDULAR SECRETORY SYSTEM in *Cannabis* was first described during the 19th century as a lipophilic type producing abundant essential oils and resins in association with external glandular hairs (Martius, 1855; Unger, 1866; Flückiger and Hanbury, 1878; Tschirch, 1889). Morphologically, a variety of gland hair types including small, bulbous as well as large, tall-stalked or stalkless capitate forms have been described from light microscopic and most recently from scanning electron microscopic investigations (Hammond and Mahlberg, 1973, 1977). Morphological interest in the glandular hairs has persisted not only from their potential in illuminating problems of *Cannabis* systematics and forensic identification, but more basically because of their chemobotanical association with the active natural product, tetrahydrocannabinol (Bouquet, 1950; Fujita et al., 1967; Fairbairn, 1972; Malingré et al., 1975; Turner, Hemphill, and Mahlberg, 1977).

Little is known about the structure of these glands in relation to their functional secretory activity. Bouquet (1950) noted from light microscopy the large nucleus and dense protoplasm of young glands and described the secretion of an oleoresin in mature glands which became stored beneath a distended cuticle. Abundant glandular secretion often resulted in the rupture of the cuticle and the spreading of the resin over the gland surface. Formation of an external secretory cavity by separation of the cuticle from secretory cells was generally accepted by early workers and was incorporated into Hayward's (1938) review of the structure of *Cannabis*.

DePasquale (1974), in a brief treatment of gland ultrastructure in *Cannabis*, described the accumulation of an osmiophilic material, assumed to be the secretory product, within a large vacuole system of the secretory cells. Secretion was believed to occur by emptying of the vacuoles and exiting of the product through existing pores in the wall and cuticle layers.

Our investigations on the ultrastructure of *Cannabis* were initiated to elucidate the development of the protoplast in the glands and its functional relationships to the secretory process in this lipophilic glandular system.

MATERIALS AND METHODS—Plants of a Mexican, high drug-producing strain of *Cannabis sativa* L. were derived and cultured as previously described (Hammond and Mahlberg, 1973). All observations were made from developing bracts which ensheath the ovary of pistillate plants.

Bracts were prepared for transmission electron microscopy (TEM) by fixation overnight at room temperature in a 4% glutaraldehyde solution con-

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taining picric acid (Turner, 1970). After fixation, tissues were washed in 0.05 M sodium cacodylate buffer (pH 7.2), post-fixed with 2% OsO_4 vapor for 2 hr, soaked in 1% aqueous uranyl acetate, dehydrated in ethanol followed by acetone, and embedded in Spurr low-viscosity resin (Spurr, 1969). Thin sections were cut on a Sorvall T-2 ultramicrotome, post-stained with uranyl acetate and lead citrate, and viewed with a Hitachi HU-11C electron microscope at 50 kV accelerating voltage.

A periodic acid-silver method was used for EM localization of polysaccharides (Hayat, 1970; Marinozzi, 1961; Rambourg and Leblond, 1967). Thin sections were mounted on formvar coated gold grids and treated with 1% aqueous periodic acid for 15 min. Sections were then washed and incubated in a silver methenamine solution at 60 C in the dark for 30 min, washed, soaked in 3% sodium thiosulfate at room temperature for 5 min, washed again, dried, and viewed without post-staining. Control sections were treated as above, but incubated in the absence of silver methenamine to check on the complete oxidation of the OsO_4 post-fixative.

A variation of the above procedure, the periodic acid-chromic acid-silver method (Hayat, 1970), was used as a selective cytoplasmic membrane stain. The staining procedure is similar to that for the periodic acid-silver method with the addition of a 10% aqueous chromic acid treatment for 5 min following the periodic acid oxidation.

OBSERVATIONS—*Early gland ontogeny*—The glandular covering of mature bracts is characterized by an abundance of capitate-sessile and capitate-stalked gland types. In addition to glands, numerous nonglandular trichomes also are present on the bract. Capitate-stalked glands arise relatively late in bract development as compared to capitate-sessile glands (Hammond and Mahlberg, 1977) and are thus more frequently encountered in early stages of their development surrounded by more mature capitate-sessile glands (Fig. 3). Gland initials can be clearly distinguished from nonglandular trichome initials which develop a specific directional orientation to the tip of the bract and by their characteristic wall thickenings. Capitate-stalked gland initiation begins as a vertical enlargement of an epidermal initial (Fig. 1). This initial divides first anticlinally (Fig. 2), bisecting the initial, then periclinally (Fig. 3), delimiting an upper pair of cells which form the secretory portion and a lower pair of cells which form the auxillary portion. The secretory portion is delimited very early in gland development and will be segmented by additional anticlinal divisions into a 8–13-celled secretory disc (Fig. 5). The auxiliary portion, which will mature into a short, few-celled support for the secretory disc, further develops by a periclinal division which divides it into an upper stipe cell layer and a lower base cell layer (Fig. 4). Capitate-stalked gland development continues with the formation of a secretory cavity (Fig. 6) followed by a proliferation of adjacent epidermal cells which form a tall multicellular stalk that lifts the gland proper (secretory cells, stipe cells, base cells) above the bract surface (Fig. 7).

Pre-secretory stages of gland development—The ultrastructure of capitate-stalked gland initials closely resembles that of surrounding protodermal cells in that they possess a dense ground substance with a large central nucleus (Fig. 1). Gland initials, however, are distinguishable from adjacent protodermal cells by their early radial enlargement. Additionally, the vacuolar system is frequently less well developed than in other nonglandular protodermal cells (Fig. 2) and the initial contains few endoplasmic reticulum (ER) elements, dictyosomes, or plastids. Plastids when encountered in gland initials, have a poorly developed internal membrane system compared to chloroplasts of adjacent protodermal cells.

In the older 4-celled disc stage, the secretory cells are characterized by numerous spherical lipid bodies which vary in size and degree of electron density, and an extensive cytoplasmic fibrillar system (Fig. 10). Lipid bodies are frequently found in close association with mitochondria, ER, and the fibrillar material.

The fibrillar material consists of compact bundles of unbranched parallel filaments, approximately 0.01 μm in diam that ramify throughout the cytoplasm (Fig. 10). Filaments appeared as rods of variable length in longisection and as dots in transection (Fig. 9). Both the lipid bodies and the fibrillar material are ephemeral and disappear well before the onset of secretory activity.

Plastids in gland cells of the 4-celled stage are spherical in shape, 1.5 μm in diam and lack a granal lamellar system. Plastids frequently accumulate an electron dense material within the stroma and at scattered locations within the plastid envelope (Fig. 10).

In glands at an 8–13-celled disc stage, and just prior to onset of secretory activity, the cytoplasm of the disc cells is highly electron dense as compared to cytoplasm in adjoining auxiliary and dermal cells (Fig. 5, 6). This increase in electron density may reflect an increase in ribosomes within the secretory cells. At this stage plastids and mitochondria are abundant and dictyosomes and dictyosome-derived secretory vesicles are few in number (Fig. 12). The plastids are elongate in shape and have a dense stroma. Frequently

plastids contain rudimentary internal membranes consisting of isolated lamellae in small clusters or short dilated strands.

Secretory cells in their transition from the 4- to 8–13-celled state develop a large central vacuole that appears to be derived from ER. ER participation is suggested by regions of ER cisternae which have become dilated (Fig. 11, between arrows) and by the presence of flattened portions of larger vacuoles which appear to have arisen from further dilation of lamellar sheets. Dilation of ER into small vacuoles and subsequent continued dilation and/or fusion of these vacuoles (Fig. 5, 6) could account for the appearance of the large central vacuole characteristic of mature secretory cells (Fig. 7, 8). Prior to the onset of secretion, the large central vacuole accumulates an electron dense material that typically occurs along the inner surface of the vacuole membrane (Fig. 6, 7). Localization of this material within the vacuole, as opposed to an acumulation on the outer surface of the vacuole membrane, is demonstrated by staining of the vacuole membrane with the periodic acid-chromic acid-silver method (Fig. 8).

Secretory cells prior to the onset of secretion also proliferate an abundance of tubular and branched ER scattered within the cytoplasm (Fig. 12). The origin of ER at this stage may be from the nuclear envelope as suggested by ER-nuclear membrane connections (Fig. 12, arrow).

A distinctive feature of the *Cannabis* glandular system is the development of a symplast within the secretory disc. Large, intercellular cytoplasmic connections develop between cells of the secretory disc (Fig. 5, 7, arrows). These connections are often large enough for the free exchange of cellular organelles. Intercellular cytoplasmic connections of this type were never observed between secretory cells and the underlying auxiliary cells or between the auxiliary cells themselves. The absence of these large cytoplasmic connections in early gland stages and the evidence of wall removal at plasmodesmata sites (Fig. 10, arrows) suggests that their formation results from removal of existing walls rather than from incomplete wall formation in cytokinesis.

Secretory stages of gland development—Gland secretory activity commences with the production and extrusion of a secretory product resulting in the initiation of a secretory cavity (Fig. 6). Production of the scretory product is closely associated with developmental changes in plastids which at this time greatly increase in number and structural complexity (Fig. 13). Plastids, initially containing a dense stroma and few internal membranes, gradually form a complex, paracrystalline membranous inclusion as they mature. Layers of membrane are observed in the stroma which appear to become incorporated into a highly ordered membrane system which closely resembles a prolamellar body (Fig. 15). Unlike a prolamellar body, the paracrystalline body in *Cannabis* continues to grow in size until it occupies nearly all of the open stroma area of the mature plastid (Fig. 14, 16). The pattern of membrane organization observed within the paracrystalline body will vary with the plane of section through its three-dimensional structure. At maturity plastids cease to divide and assume a spherical shape 1.4–1.6 μm in diam.

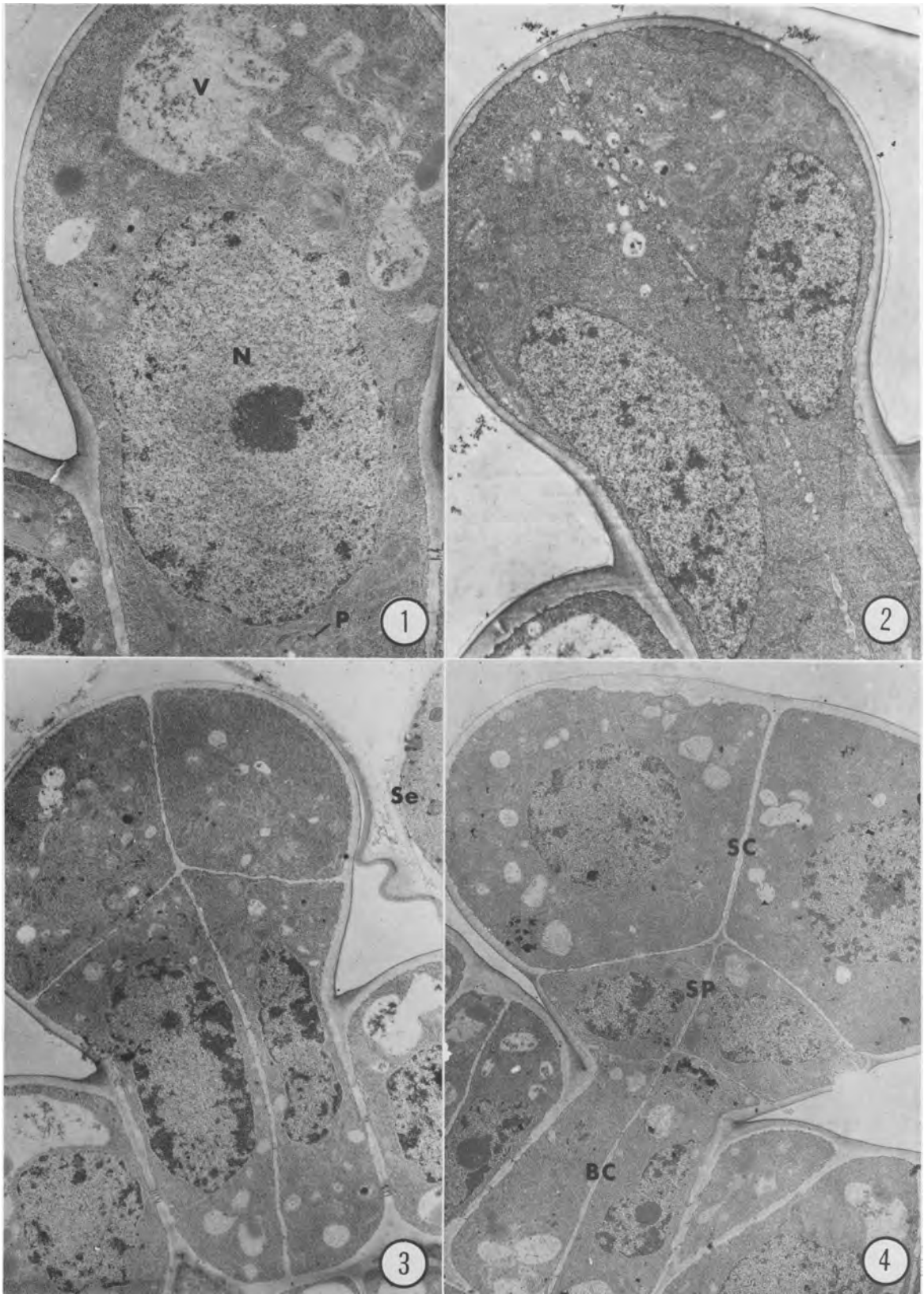
Plastids containing a paracrystalline body are restricted to secretory cells of the glandular disc.

KEY TO LABELING: BC, base cell(s); CW, cell wall; D, dictyosome; ER, endoplasmic reticulum; F, fibrillar material; L, lipid body; L_1, cuticle layer; L_2, middle wall layer; L_3, inner wall layer; M, mitochondrion; MS, multicellular stalk; N, nucleus; P, plastid; PS, secretory product; S, secretory cavity; SC, secretory cell(s); Se, capitate-sessile gland; SP, stipe cell(s); SM, sheath; V, vacuole.

Fig. 1–4. Early development of capitate-stalked glands. **1.** Gland initial. ×6,400. **2.** Two-celled gland stage from anticlinal division of initial cell. ×9,000. **3.** First periclinal division in gland creating upper secretory portion and lower auxiliary portion. ×4,100. **4.** Periclinal division in auxiliary portion establishing upper stipe cells which support gland head and lower base cells which are embedded in epidermis. ×3,900.

Fig. 5–8. Mid and late stages in capitate-stalked gland development. **5.** Anticlinal divisions in secretory portion produce multicellular secretory disc. Note large cytoplasmic connections between cells of secretory disc (arrows). ×1,400. **6.** Stage in gland secretion and formation of secretory cavity. Note portion of secretory cavity formed above a few secretory cells and further wall wrinkling above adjacent secretory cells. ×3,300. **7.** Mature gland with gland proper (base, stipe, and secretory cells) positioned atop multicellular stalk. ×1,200. **8.** Large central vacuole with included osmiophilic material. ×8,300.

Fig. 9–12. Ultrastructure of secretory cells prior to secretion stage. **9.** Fibrillar material with filaments in trans- and longisection. ×21,000. **10.** Young 4-celled secretory disc stage. Arrow points to one of several plasmodesmata sites where wall perforation may be occurring. Secretory cells contain lipid bodies, plastids, and fibrillar material. ×10,300. **11.** Early development of vacuole system by dilation of ER (several lamellae between arrows) and dilation of lamellar sheets. ×10,200. **12.** Secretory cells just prior to secretion. ×19,600.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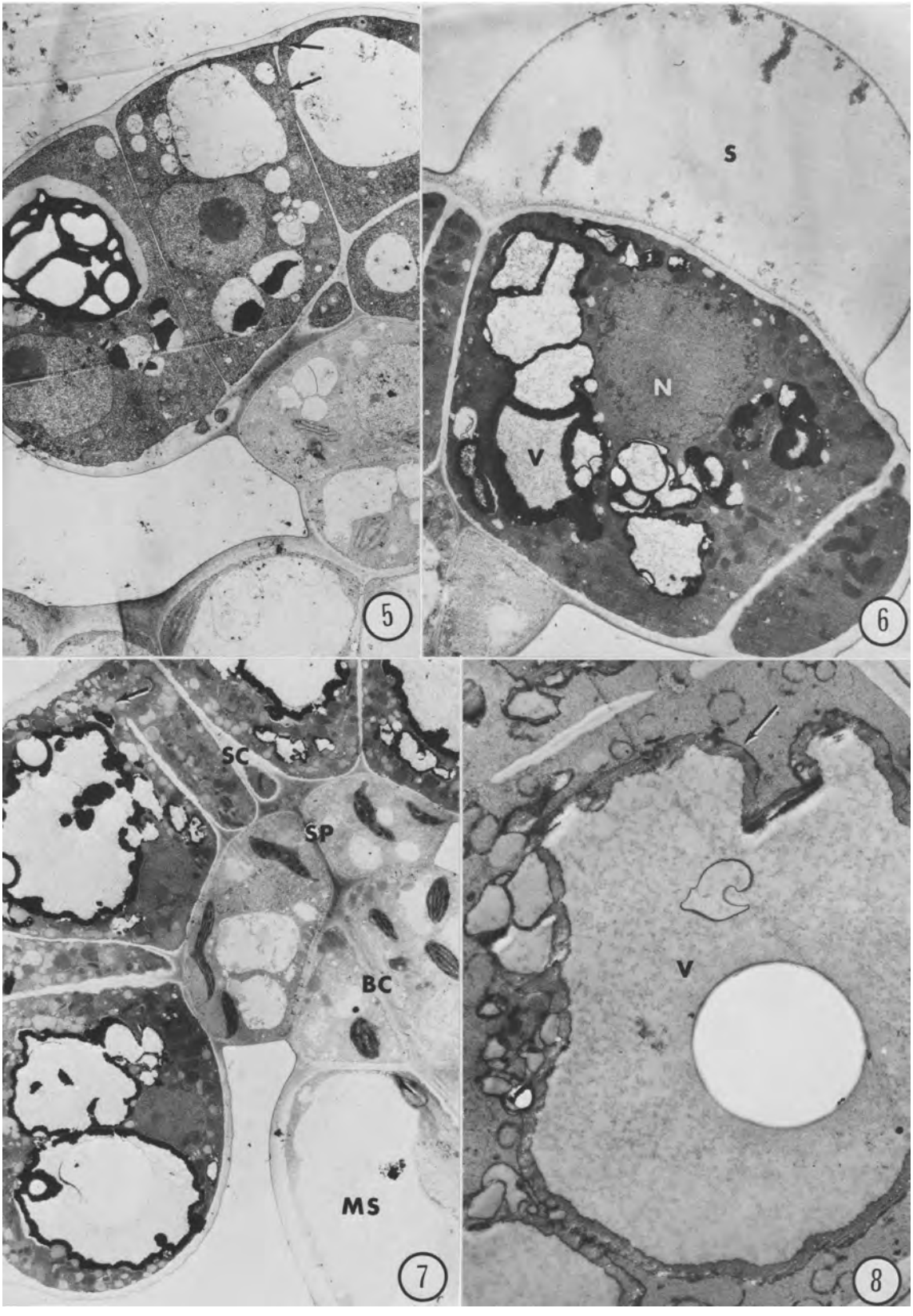
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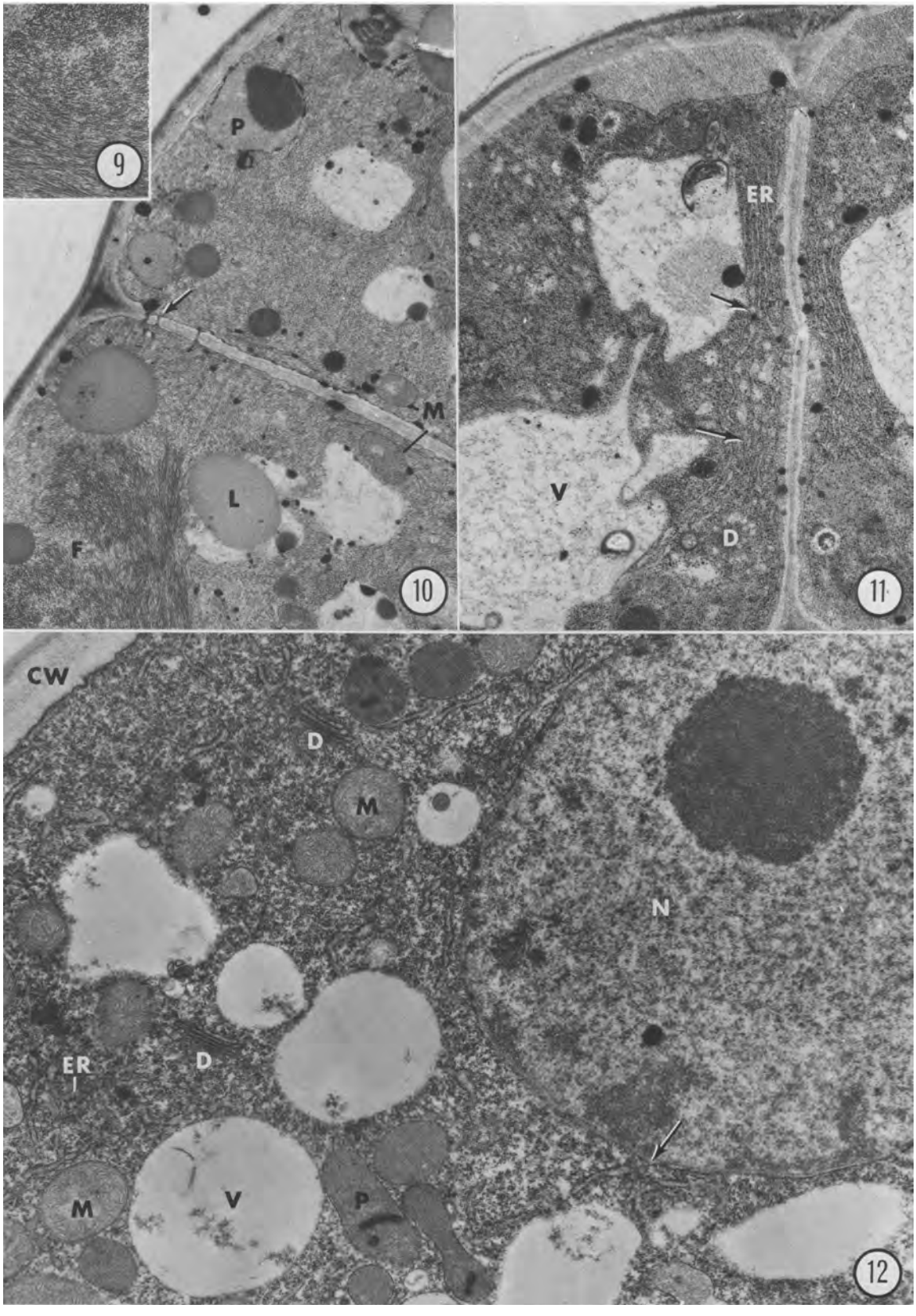
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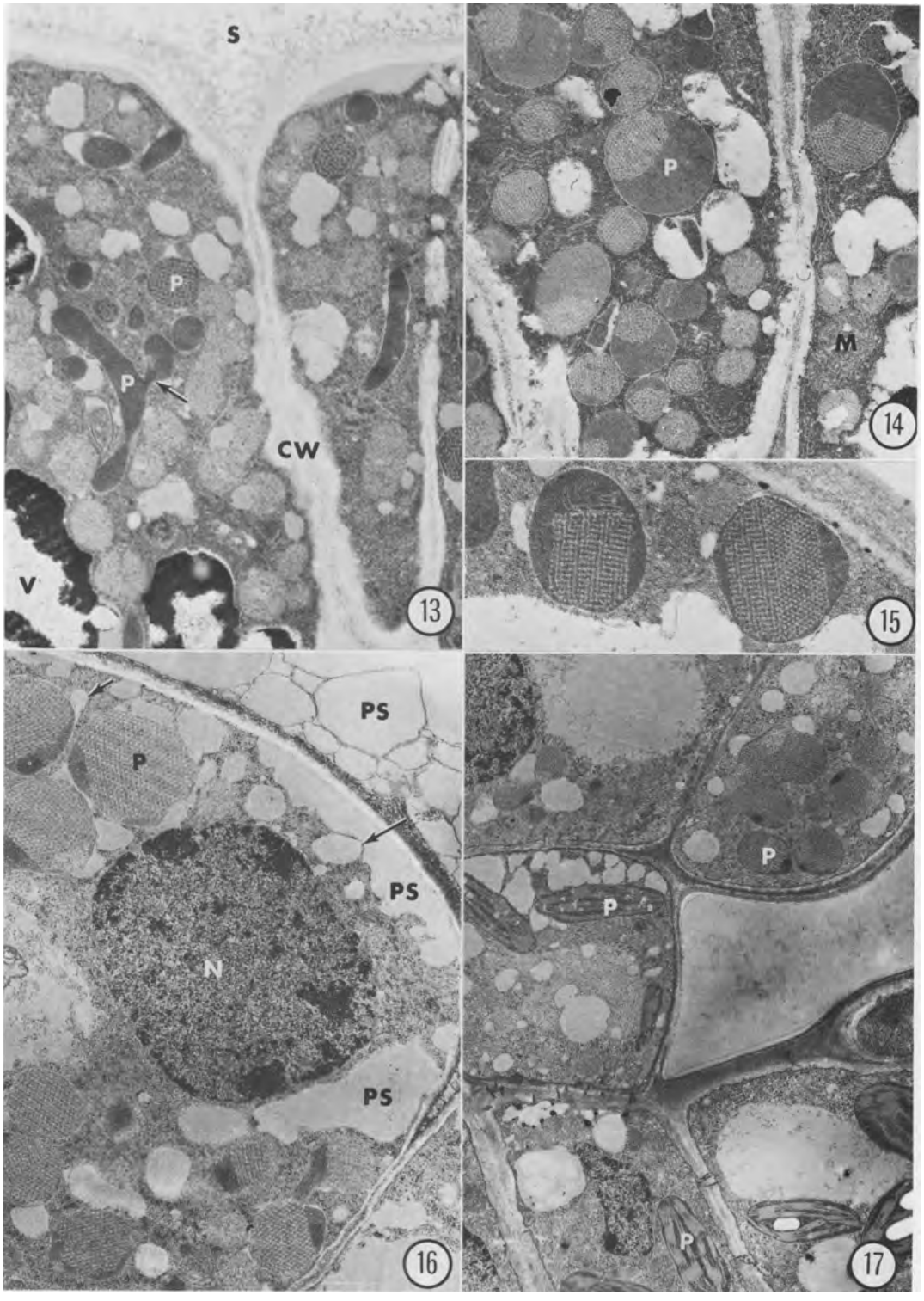
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Cells of the auxiliary portion of the gland and surrounding epidermal cells contain typical chloroplasts, although starch accumulates only in epidermal plastids (Fig. 17). Occasionally, chloroplasts of the stipe cells become greatly elongated to more than twice their normal length.

Plastids of the secretory cells appear to be the probable source of the main secretory product. Material interpreted as a secretion appears at the surface of immature plastids as a narrow zone of electron transparent material (Fig. 14, 15). An increasing quantity of similar material aggregates along the periphery of the plastids as they mature (Fig. 16, short arrow) and then migrates through the cytoplasm and accumulates along the cell surface adjoining the secretory cavity (Fig. 16, long arrow). This product does not appear to be membrane bound and may fuse with other aggregations of similar products in route to and at the cell surface.

Formation of the secretory cavity—A single, large secretory cavity forms over the secretory disc by a process involving separation within the outer wall layers of the disc (Fig. 6, 19). Formation of the secretory cavity and its outer bounding layer, the sheath, begins as a swelling and loosening within the cell walls. As secretion begins, the sheath becomes folded and wrinkled, and with continued accumulation of secretory material (Fig. 6) this layer becomes stretched to form the boundary of the secretory cavity (Fig. 6). Under conditions of growth in this study the sheath layer did not rupture.

The secretory product within the secretory cavity, although subject to extraction by standard EM methods, becomes organized during gland development into closely packed spherical bodies of large (4–5 μm diam) and small (0.1–0.3 μm diam) size (Fig. 18). The spherical secretory bodies seem to be delimited by a membrane-like structure. This is suggested because the spherical bodies remain distinct despite being in contact under pressure and because a boundary of some nature has been stabilized by fixation and subsequently stained.

The organization of the secretory product into the spherical bodies must occur in the secretory cavity and not within the secretory cells because extrusion of the product occurs directly through the intact cell wall and cell membrane barrier.

Structure of the sheath layer—At the time of wall separation and sheath formation, the cell wall of the secretory disc surface is conspicuously multilayered (Fig. 6, 19). The wall is comprised of three distinct layers which vary in density and texture. The outer, thin, amorphous layer is believed to be cuticle (Fig. 19, L_1). Beneath this layer is a middle layer in which wall separation occurs to form the secretory cavity (Fig. 19, L_2). A portion of this layer along with the cuticular layer will form the relatively thick sheath layer. The innermost layer (Fig. 19, L_3) of the three-layered wall is a portion of the primary cellulosic wall of the secretory cells.

The sheath layer was suspected to be comprised of both cuticle and a portion of the primary cell wall because of its bilayered ultrastructure and its relatively thick and elastic nature. The existence of a polysaccharide layer, presumably cellulose, beneath the cuticle layer in the sheath was demonstrated histochemically using the periodic acid-silver method. Comparison of cell wall staining of treated tissues (Fig. 21) with epidermal cell walls of control tissues (Fig. 20) demonstrates the specificity of the stain for cellulosic walls in this material. Sheath layers stained with periodic acid-silver show a conspicuous layer of silver deposited beneath the unstained cuticular layer (Fig. 21, 22, between arrows). The lightness of the silver staining suggests a layer not wholly composed of cellulose. Interestingly, the membranes of the secretory bodies also stain lightly with silver deposits.

DISCUSSION—Glandular secretory systems, despite their structural diversity, are broadly classifiable on the basis of function into either lipophilic or hydrophilic types (Uphof, 1962; Schnepf, 1974). Lipophilic glands, which are poorly understood, include glands which secrete terpenes (essential oils and resins), waxes, and fats.

Lipophilic glands of the terpene type have been studied ultrastructurally in a number of species and are characterized by their dense ribosomal groundplasm and extensive, often

Fig. 13–17. Ultrastructure of secretory cells during secretory stage. **13.** Early secretory stage with well-formed secretory cavity. Plastids increase in number by pinching process (arrow) and begin to organize a paracrystalline inclusion. ×11,000. **14.** Mid stage in secretory activity. Plastids are dominant organelle and most contain a well-developed paracrystalline body. ×10,800. **15.** Plastids with growing and well-developed paracrystalline bodies. ×13,300. **16.** Late stage in secretory activity. Numerous plastids with secretion product at their surface and stages of migration and accumulation of secretory product along cell surface adjoining secretory cavity. ×12,500. **17.** Comparison of plastids in gland cells and surrounding epidermal cells. ×6,800. See p. 142 for Key to Labeling.

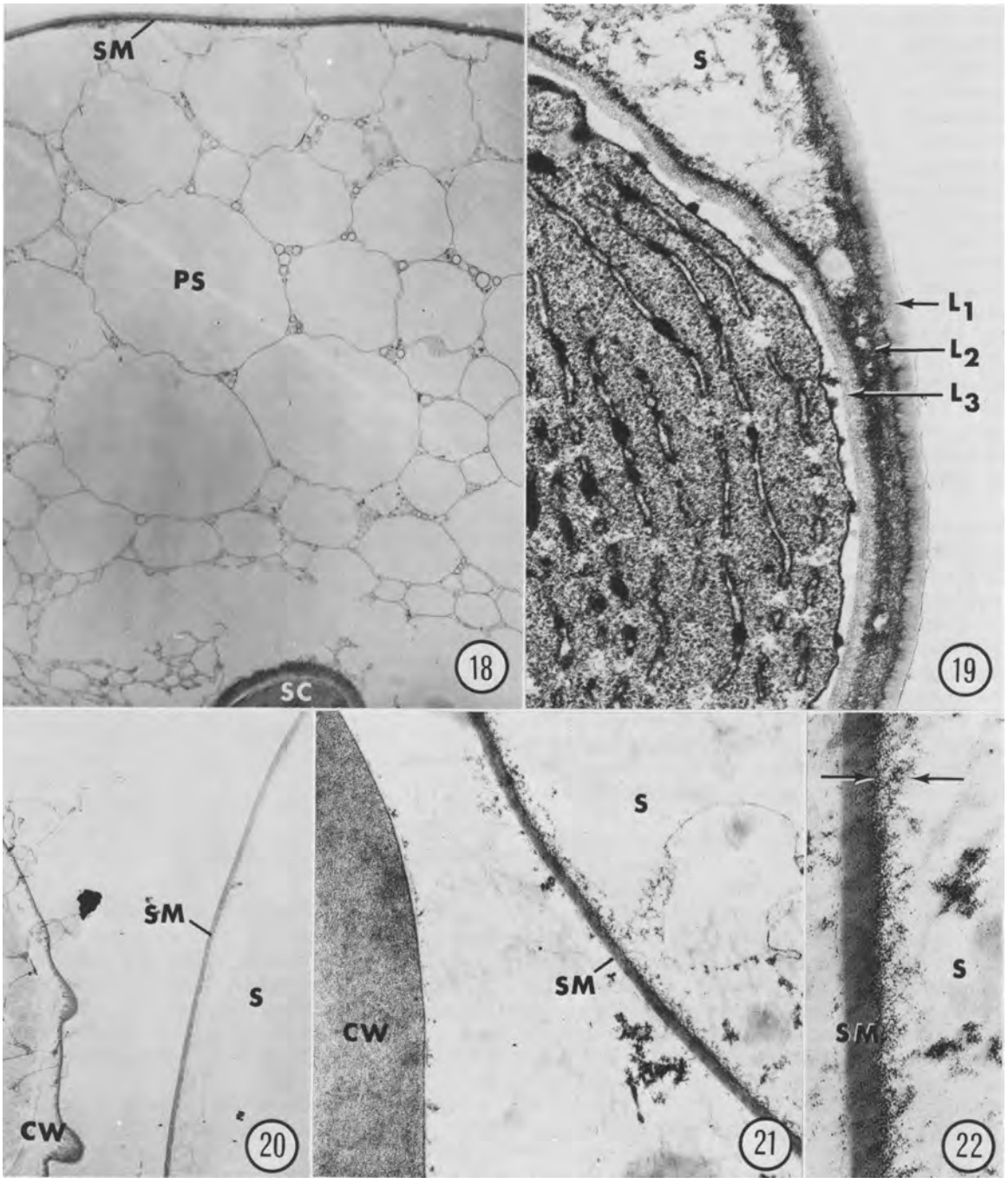

Fig. 18–22.—Fig. 18, 19. Organization of the secretory product and formation of the secretory cavity. **18.** Secretory product of spherical bodies of varying size. Organization suggests partitioning of lipophilic material within aqueous phase. ×4,900. **19.** Formation of secretory cavity by separation in middle layer of three-layered cell wall. ×32,100.—Fig. 20–22. Histochemical staining with periodic acid-silver method to demonstrate polysaccharides. **20.** Control section unstained with silver to demonstrate lack of prior staining in sheath and cell walls. ×3,900. **21.** Treated sections showing silver staining of epidermal cell wall and inner portion of sheath. ×12,200. **22.** Close up of silver stained inner portion of sheath (between arrows) and unstained outer cuticular portion. ×36,200. See p. 142 for Key to Labeling. We thank Dr. F. R. Turner for Fig. 19.

massive, development of smooth ER during the secretion phase (Amelunxen and Arbeiter, 1969; Schnepf, 1969a, 1969b; Wollenweber and Schnepf, 1970; Dell and McComb, 1975). In other terpene secreting glands the ER is less well developed and leucoplasts become the most prominent organelle during secretion (Heinrich, 1966; Amelunxen and Arbeiter, 1967; Amelunxen and Gronau, 1969). The leucoplasts, which typically lacked well-developed thylakoid systems, were observed to accumulate lipophilic materials which were then released with the breakdown of the plastids and general degeneration of the secretory cells. Although sites of localization of terpenes can be identified, the nature of the secretory process is often not clearly defined. In some glands, such as *Pinus* resin duct epithelial cells (Wooding and Northcote, 1965), terpene synthesis may be more complex, involving both elements of the ER and leucoplasts in conjunction or separately as steps in the elaboration and secretion of the product.

The *Cannabis* glandular system is a terpene type producing mono- and sesquiterpene essential oils and a series of terpenophenolic compounds, the cannabinoids, which includes the marijuana hallucinogen, tetrahydrocannabinol (Hegnauer, 1964; Mechoulam, 1970; Hendriks et al., 1975; Malingré et al., 1975). The ultrastructure of *Cannabis* glands fits the general pattern for terpene secreting glands in having a dense ground plasm, abundant ER, and numerous leucoplasts. However, *Cannabis* displays several distinctive ultrastructural and functional features not previously reported for *Cannabis* or other lipophilic glands. Foremost among these features is the development and function of its highly modified plastids. The plastids in presecretory stages resemble typical leucoplasts with few internal membranes, but with the onset of secretion undergo a rapid and extensive increase in number and develop a highly organized paracrystalline body. The paracrystalline body increases in size until it nearly fills the plastid, leaving only a small open stromal area. Presumably the stroma is not obliterated, but may occupy space within the lattice of the paracrystalline body. The structure of the paracrystalline body of mature plastids, with the exception of its large size, closely resembles that described for the prolamellar body of etioplasts (Klein and Schiff, 1972) and proplastids (Gunning, 1965). The variety of membrane profiles encountered in *Cannabis* closely resemble those generated by sections of the cuboidal lattice structure of the *Avena* prolamellar body (Gunning, 1965). Functionally, the plastids in *Cannabis* are associated with a product that accumulates and migrates from their surface. The dominance of this plastid type in actively synthesizing glands, its large internal membrane surface, and its close association with a product suggests a functional role in synthesis.

DePasquale (1974), apparently unaware of the specialized plastids in *Cannabis*, related the secretion process to the accumulation and disappearance of osmophilic materials from the large vacuole system. The role of the vacuole in secreting glands is difficult to assess. Their involvement in the accumulation and secretion of a gland product, perhaps even in association with plastids or ER, certainly is possible. However, vacuoles might also function primarily in osmotic regulation or in a cell space-filling role.

A major problem in interpreting gland function in a complex system such as *Cannabis* where glands may be concurrently or sequentially elaborating several products is in identifying a specific product at a specific organelle site. This problem is compounded by the potential extraction of the lipophilic product in processing the material. Nevertheless, the observations of the extensive development and function of plastids at the time of active secretion coupled with the prior association of cannabinoids with the major secretory product (Turner, Hemphill, and Mahlberg, 1977), suggest that the unique plastid complement found in *Cannabis* may play a role in the synthesis or elaboration of the marijuana cannabinoids. This relationship can be established with certainty only by future ultrastructural studies which histochemically localize cannabinoids at specific cytomembrane sites.

Ultrastructural observations of developing glands contributes to an understanding of the formation of the secretory cavity and the secretory process. The relatively thick and tough sheath enclosing the secretory product is now shown for *Cannabis* to consist not of cuticle alone, but of cuticle and a portion of its associated primary wall. Wall separation begins presumably by enzymatic breakdown of a middle wall layer perhaps rich in pectin. Actual separation of the wall and initiation of the secretory cavity begins with the accumulation of the secretory product. The symplastic condition formed by cytoplasmic connections within the secretory disc may account for the coordinated separation which occurs along the entire outer surface of the secretory disc. Sheath formation by separation within an outer wall layer has also been described for capitate glands of *Silene* (Fridvalszky, Rakovan, and Keresztes, 1970) and *Mentha* (Amelunxen, 1965). In *Mentha*, Amelunxen considered the sheath to be composed of a cuticle and a "cuticular layer" which separated from the underlying primary cellulosic wall. Our ultrastructural and histochemical observations on the sheath of *Cannabis* suggest the presence of cellulose both in the sheath inner sur-

face and in the disrupted primary wall layer. This may have bearing on the secretion process. The rapid and extensive movement of lipophilic materials from the cell cytoplasm to the external secretory cavity may be facilitated by the disruption of the intervening wall layer. DePasquale (1974) noted the three-layered structure of the wall in the secretory disc of *Cannabis* but described secretion as occurring through preexisting pores within the cell wall and cuticle. We have not observed pores in either the cell wall or sheath layer.

The secretory product accumulating within the secretory cavity is structurally organized into spherical bodies of varying size bounded by a membrane layer. Recognizing the difficulties of constructing and regulating an extensive membrane system external to the cell protoplast, we believe that the spherical bodies are delimited by half unit membranes (Yatsu and Jacks, 1972; Kwiatkowska, 1973). In this system, the membrane would be constructed entirely of lipid in which an artificial membrane is created by partitioning of the lipophilic product in an aqueous environment. Such a membrane model could account for its formation by self-assembly in an external cellular environment as well as stabilization of its structure by osmium fixation. An added dimension to the structure of this membrane is suggested by observations of its silver-methenamine staining properties. This histochemical test is not completely specific for polysaccharides, but also certain amino acids can become stained by this method (Nicolet and Shinn, 1939). Thus, the possibility exists for a more structurally complex membrane than previously envisioned.

LITERATURE CITED

AMELUNXEN, F. 1965. Elektronenmikroskopische Untersuchungen an den Drüsenschuppen von *Mentha piperita* L. Planta Med. 13: 457–473.

———, AND H. ARBEITER. 1967. Untersuchungen an den Spritzdrüsen von *Dictamnus albus* L. Z. Pflanzenphysiol. 58: 49–69.

———, AND ———. 1969. Untersuchungen an den Drüsenhaaren von *Cleome spinosa* L. Z. Pflanzenphysiol. 61: 73–80.

———, AND G. GRONAU. 1969. Elektronenmikroskopische Untersuchungen an den Ölzellen von *Acorus calamus* L. Z. Pflanzenphysiol. 60: 156–168.

BOUQUET, R. J. 1950. *Cannabis*. Bull. Narcotics 2: 14–30.

DELL B., AND A. J. MCCOMB. 1975. Glandular hairs, resin production, and habitat of *Newcastelia viscida* E. Pritzel (Dicrastylidaceae). Aust. J. Bot. 23: 373–390.

DEPASQUALE, A. 1974. Ultrastructure of the *Cannabis sativa* glands. Planta Med. 25: 238–248.

FAIRBAIRN, J. W. 1972. The trichomes and glands of *Cannabis sativa* L. Bull. Narcotics 24: 29–33.

FLÜCKIGER, F. A., and D. HANBURY. 1878. Histoire des drouges d'origine végétale. V. 2. Octave Doin, Editeur, Paris.

FRIDVALSZKY, L., J. N. RAKOVAN, AND A. KERESZTES. 1970. Development of the glandular cell in the epidermis of *Silene armeria*. V. 3, p. 427–428. *In* P. Favard [ed.], International Conference on Electron Microscopy, 7, Grenoble, France. Société Francaise de Microscopie Electronique, Paris.

FUJITA, M., S. HIROKO, E. KURIYAMA, M. SHIGEHIRO, AND M. AKASU. 1967. Studies on *Cannabis*. II. Examination of the narcotic and its related components in hemps, crude drugs, and plant organs by gas-liquid chromatography and thin-layer chromatography. Annu. Rep. Tokyo Coll. Pharm. 17: 238–242.

GUNNING, B. E. S. 1965. The greening process in plastids. 1. The structure of the prolamellar body. Protoplasma 60: 111–130.

HAMMOND, C. T., AND P. G. MAHLBERG. 1973. Morphology of glandular hairs of *Cannabis sativa* from scanning electron microscopy. Amer. J. Bot. 60: 524–528.

———. 1977. Morphogenesis of capitate glandular hairs of *Cannabis sativa* L. (Cannabaceae). Amer. J. Bot. 64: 1023–1031.

HAYAT, M. A. 1970. Principles and techniques of electron microscopy. Biological applications. V. 1. Van Nostrand Reinhold, New York.

HAYWARD, H. E. 1938. The structure of economic plants. MacMillan, New York.

HEGNAUER, R. 1964. Chemotaxonomie der Pflanzen. Birkhäuser Verlag, Stuttgart.

HEINRICH, G. 1966. Licht- und elektronenmikroskopische Untersuchungen zur Genese der Exkrete in den lysigenen Exkreträumen von *Citrus medica*. Flora 156: 451–456.

HENDRIKS, H., T. M. MALINGRÉ, S. BATTERMAN, AND R. BOS. 1975. Mono- and sesqui-terpene hydrocarbons of the essential oil of *Cannabis sativa*. Phytochemistry. 14: 814–815.

KLEIN, S., AND J. A. SCHIFF. 1972. The correlated appearance of prolamellar bodies, protochlorophyll (ide) species, and the Shibata shift during development of bean etioplasts in the dark. Plant Physiol. 49: 619–626.

KWIATKOWSKA, M. 1973. Half unit membranes surrounding osmiophilic graules (lipid droplets) of the so-called lipotubuloid in *Ornithogalum*. Protoplasma 77: 473–476.

MALINGRÉ, T., H. HENDRIKS, S. BATTERMAN, R. BOS, AND J. VISSER. 1975. The essential oil of *Cannabis sativa*. Planta Med. 28: 56-61.

MARINOZZI, V. 1961. Silver impregnation of ultrathin sections for electron microscopy. J. Biophys. Biochem. Cytol. 9: 121–133.

MARTIUS, G. 1855. Pharmakologisch-Medicinische Studien über den Hanf. Junge und Sohn, Erlangen.

MECHOULAM, R. 1970. Marihuana chemistry. Science 168: 1159–1166.

NICOLET, B. H., AND L. A. SHINN. 1939. The action of periodic acid on α-amino alcohols. J. Amer. Chem. Soc. 61: 1615.

RAMBOURG, A., AND C. P. LEBLOND. 1967. Electron microscope observations on the carbohydrate-rich cell coat present at the surface of cells in the rat. J. Cell Biol. 32: 27–53.

SCHNEPF, E. 1969a. Über den Feinbau von Öldrüsen. I. Die Drüsenhaare von *Arctium lappa*. Protoplasma 67: 185–194.

1969b. Über den Feinbau von Öldrüsen. II Die Drüsenhaare in *Calceolaria*-Blüten. Protoplasma 67: 195–203.

———. 1974. Gland cells. *In* A. W. Robards [ed.], Dynamic aspects of plant ultrastructure, p. 331–357. McGraw-Hill, New York.

SPURR, A. 1969. A low-viscosity epoxy resin embedding medium for electron microscopy. J. Ultrastruct. Res. 26: 31–43.

TSCHIRCH, A. 1889. Angewandte Pflanzenanatomie. Band 1. Urban und Schwarzenberg, Wien.

TURNER, F. R. 1970. The effects of colchicine on spermatogenesis in *Nitella*. J. Cell Biol. 46: 220–234.

TURNER, J. C., J. K. HEMPHILL, AND P. G. MAHLBERG. 1977. Gland distribution and cannabinoid content in clones of *Cannabis sativa* L. Amer. J. Bot. 64: 687–693.

UNGER, F. 1866. Grundlinien der Anatomie und Physiologie der Pflanzen. Bramüller, Wien.

UPHOF, J. C. Th. 1962. Plant hairs. *In* W. Zimmerman and P. G. Ozenda [ed.], Encyclopedia of plant anatomy. V. 4, pt. 5, p. 1–206. Grebrüder Borntraeger, Berlin.

WOLLENWEBER, E., AND E. SCHNEPF. 1970. Vergleichende Untersuchungen über die flavonoiden Exkrete von "Mehl"-und "Öl"-Drüsen bei Primeln und die Feinstruktur der Drüsenzellen. Z. Pflanzenphysiol. 62: 216–227.

WOODING, F. B. P., AND D. H. NORTHCOTE. 1965. The fine structure of the mature resin canal cells of *Pinus pinea*. J. Ultrastruct. Res. 13: 233–244.

YATSU, L. Y., AND T. J. JACKS. 1972. Spherosome membranes. Plant Physiol. 49: 937–943.