Amer. J. Bot. 64(8): 1023–1031. 1977.

MORPHOGENESIS OF CAPITATE GLANDULAR HAIRS OF CANNABIS SATIVA (CANNABACEAE)[1]

CHARLES T. HAMMOND AND PAUL G. MAHLBERG

Department of Biology, Wabash College, Crawfordsville, Indiana 47933; and Department of Plant Sciences, Indiana University, Bloomington 47401

ABSTRACT

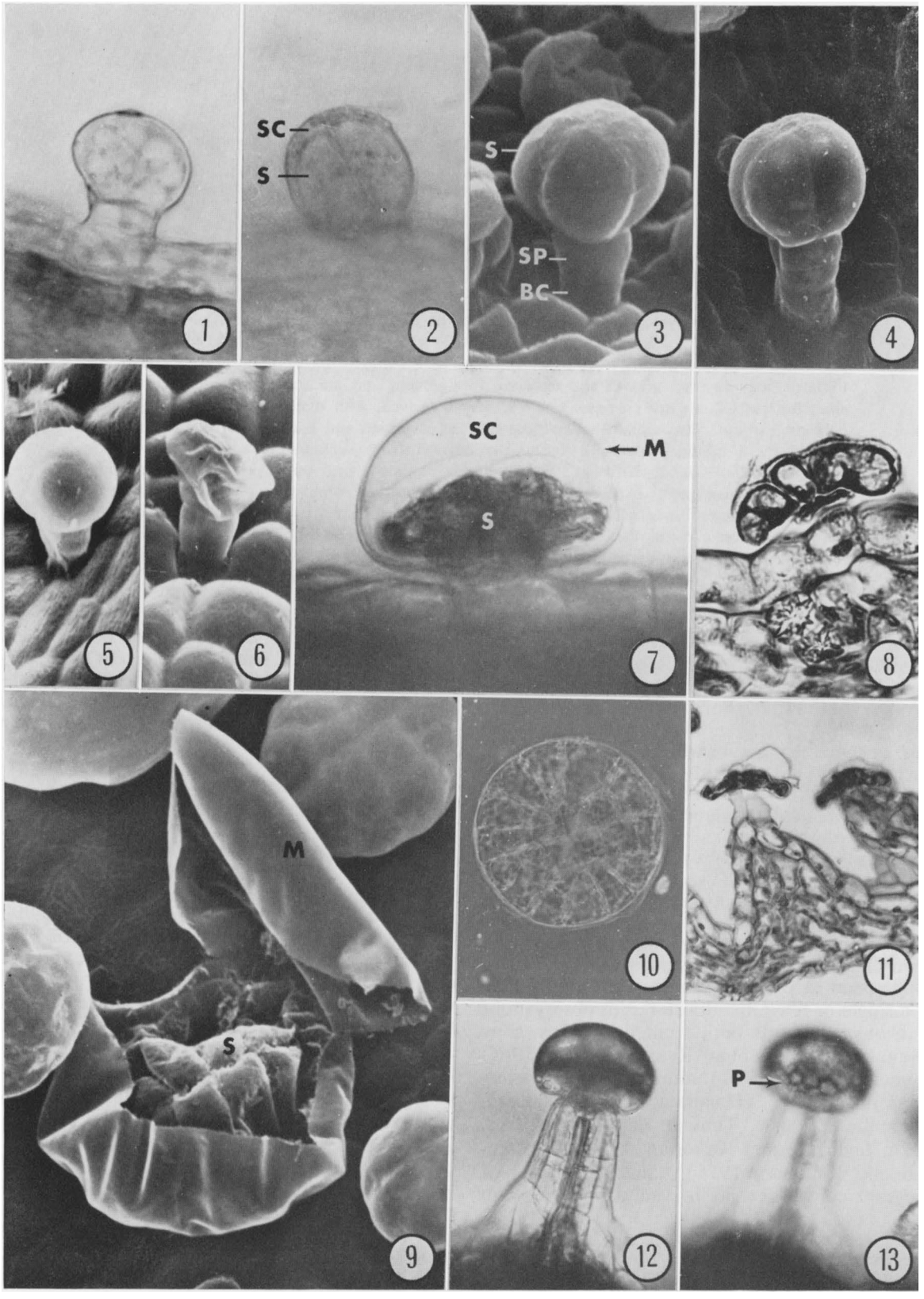
The glandular secretory system in *Cannabis sativa* L. (marihuana) consists of three types of capitate glandular hairs (termed bulbous, capitate-sessile, and capitate-stalked) distinguishable by their morphology, development, and physiology. These gland types occur together in greatest abundance and developmental complexity on the abaxial surface of bracts which ensheath the developing ovary. Bulbous and capitate-sessile glands are initiated on very young bract primordia and attain maturity during early stages of bract growth. Capitate-stalked glands are initiated later in bract growth and undergo development and maturation on medium, to full sized bracts. Glands are epidermal in origin and derived, with one exception, from a single epidermal initial. The capitate-stalked gland is the exception and is of special interest because it possesses a multicellular stalk secondarily derived from surrounding epidermal and subepidermal cells. Glands differentiate early in development into an upper secretory portion and a subtending auxiliary portion. The secretory portion, depending on gland type, may range from a few cells to a large, flattened multicellular disc of secretory cells. The secretory portion produces a membrane-bound resinous product which caps the secretory cells. Capitate-stalked glands are considered to be of particular evolutionary significance because they may represent a gland type secondarily derived from existing capitate-sessile glands.

GLANDULAR SECRETORY SYSTEMS of angiosperms are well known for their wide range of morphological and functional diversity (Hanstein, 1868; De Bary, 1884; Uphof, 1962; Lüttge, 1971; Levin, 1973). The glandular system in *Cannabis* was documented very early by Unger (1856), Tschirch (1889), and most extensively by Briosi and Tognini (1894) as an external secretory type consisting of capitate glandular hairs which produced a resinous product. Three main forms of secretion bearing glands were described and illustrated by Briosi and Tognini (1894) with little attention to their developmental relationships. All glands bore heads which were either "nearly sessile" or protruding on prominent stalks. One form of the sessile type remained small in size in comparison to the other glands and bore a head of a single or few cells. More recent observations of *Cannabis* glands both from light microscopy (Bouquet, 1950; Mohan Ram and Nath, 1964; Shimomura et al., 1967) and from scanning electron microscopy (Hammond and Mahlberg, 1973; De Pasquale, Tumino, and De Pasquale, 1974; Ledbetter and Krikorian, 1975; Dayanandan and Kaufman, 1976) utilizing a range of geographical variants are basically consistent with the morphological descriptions of earlier workers. Despite considerable understanding of the morphology of this glandular system, the developmental relationship of the different glandular forms remains obscure. It is unclear to what degree these gland types are morphologically distinct. This question is important not only in understanding the nature of the glandular system in *Cannabis*, but also as a more critical means to compare geographical variants for taxonomic differences in what is seemingly a monotypic genus (Small, Jui, and Lefkovitch, 1976; Small and Cronquist, 1976). Our initial observations on gland morphology on bracts of *Cannabis* (Hammond and Mahlberg, 1973) described a regularly occurring difference in the pattern of distribution and timing of gland appearance and maturation which suggested both a need and a basis for distinguishing three types of glands. The purpose of this paper is to further describe the anatomical and developmental interrelationships of these three gland types with special emphasis given to the development of the capitate-stalked gland type.

MATERIALS AND METHODS—Plants of a Mexican, high drug producing strain of *Cannabis sativa* L. were raised from seed and maintained in a greenhouse under long day conditions following floral induction as previously described (Hammond and Mahlberg, 1973). Specimens

[1] Received for publication 20 January 1977; revision accepted 10 May 1977.

This research was supported by an NIH research grant DA00981 and by the Indiana University Foundation. D.E.A. Registration No. PI0043113 and PH0106852.


1
SC
S
2
S
SP
BC
3
4
5
6
SC
M
S
7
8
M
S
9
10
11
12
P
13

utilized in this study represent a large plant sample selected from several hundred plants periodically grown over a two year period. Specimens were prepared for light microscopic observations by a variety of standard methods which included fresh whole mounts, sectioned paraffin-embedded tissues, and thick sectioned plastic-embedded tissues.

Specimens prepared for scanning electron microscopy (SEM) were fixed in sodium cacodylate-buffered 4% glutaraldehyde or formalin-propionic acid-alcohol, processed, and critical point dried as previously described (Hammond and Mahlberg, 1973). Specimens were coated with gold-palladium on a rotoevaporatory stage and viewed at 20 kV accelerating voltage with an ETEC Autoscan scanning electron microscope.

OBSERVATIONS—*Anatomy of glandular hairs*—Three forms of glandular hairs—bulbous, capitate-sessile, and capitate-stalked—occur together in greatest abundance on the abaxial surface of bracts which ensheath the flowers of pistillate plants. These glandular hairs, although varying greatly in morphological complexity, have a similar structural organization divisible into an upper secretory portion and a subtending auxiliary portion. The secretory portion may range in complexity from one or two secretory cells (Fig. 1, 2) to a flattened multicellular layer, the secretory disc (Fig. 8). The auxiliary portion forms a short supportive axis of few cells consisting of base cells which are embedded in the epidermal surface and above them stipe cells which directly support the secretory disc (Fig. 3, 25). Mature glands (full-sized glands) possess a resinous product which accumulates between the secretory cells and an outer bounding membranous sheath (Fig. 2, 7, 13). The secretory cells along with their extruded secretory product are termed the gland head.

Bulbous glands consist of a secretory portion containing one (Fig. 1), two (Fig. 2), or four (Fig. 3, 4) secretory cells in a single layer and an auxiliary portion containing a one or two-celled base layer and a one or two-celled stipe layer (Fig. 3, 6). These glands typically have overall dimensions of 25–30 μm in height with a 20 μm diam head. Although in the auxiliary portion a two-celled base layer and a two-celled stipe layer are most common, various combinations of these restricted cell numbers may occur. On rare occasions, stipes are found with cells arranged in two layers (Fig. 4).

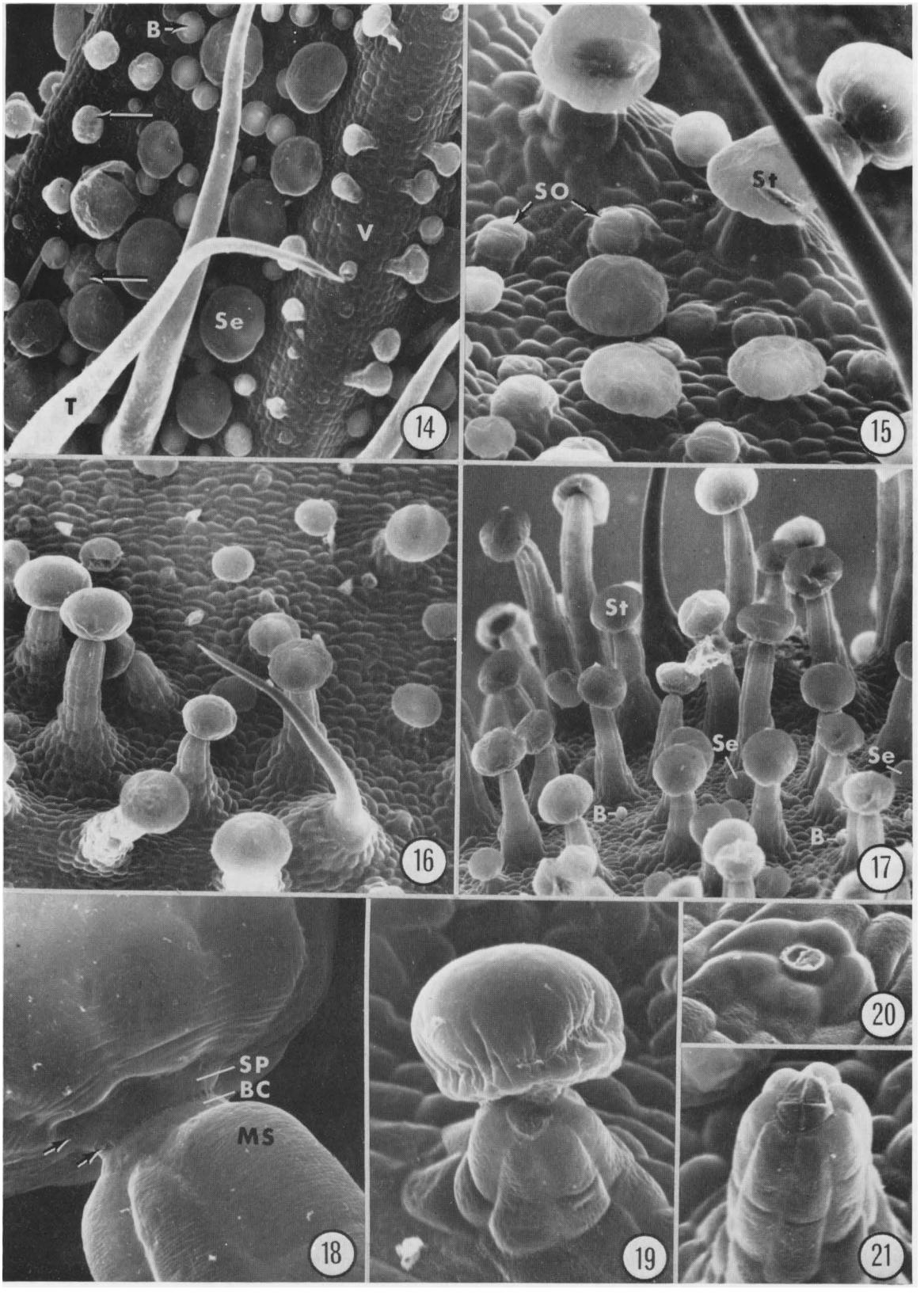
The spatial relationship of the secretory space to the underlying secretory cells is suggested in Fig. 5 which has an apparent transparent quality. The occurrence of the secretory space is suggested also by the occasional collapse of the sheath upon the secretory cells when the sheath is ruptured (Fig. 6).

Capitate-sessile glands are characterized by a large, globose glandular head 40–60 μm in diam which is two to three times the diameter of the relatively small head of the bulbous glands. Capitate-sessile glands, descriptively named because the head lacks a stalk and closely "sits upon" the bract surface, are borne upon short axes consisting of a base and a stipe layer. The head consists of a layer of secretory cells bounded by a sheath layer (Fig. 7). Secretory cells are organized into a single layer of 8–13 cells as observed in longitudinal section (Fig. 8) or in surface view (Fig. 9). In 8-celled heads (Fig. 9) a bilateral symmetry is evident with an axis parallel to the long axis of the bract. This symmetry persists, but is often obscured in heads that contain a greater cell number.

Mature capitate-stalked glands (Fig. 12, 13) may bear gland heads similar in size and structure to capitate-sessile glands, but differ in that they possess a stalk. The heads of capitate-stalked glands are frequently considerably larger than those of capitate-sessile glands and may approach 100 μm diam (Fig. 17). The stalk is secondarily derived from bract tissue and does not arise from

KEY TO LABELING: B, bulbous gland; BC, base cell; M, membranous sheath; P, secretory product; MS, multicellular stalk; S, secretory cell; SC, secretory cavity, Se, capitate-sessile gland; SO, stomate; SP, stipe cell; St, capitate-stalked gland; T, non-glandular trichome; V, vein ridge.

Fig. 1–13. Anatomy of glandular hair types from bracts of pistillate plants.—Fig. 1–6. Bulbous glands. **1.** Gland with one-celled head and slight wall separation at apex. × 990. **2.** Gland with two-celled head and small resin filled secretory cavity. × 990. **3.** Gland with four-celled head and one-celled base and stipe layers. × 1,257. **4.** Gland with four-celled head, two-celled base layer, and 2 two-celled stipe layers. × 1,130. **5.** Mature gland with two base cells, two stipe cells, and swollen gland head. The secretory cell surface is visible beneath outer sheath. × 940. **6.** Mature gland with secretory cavity disrupted and sheath collapsed. × 930.—Fig. 7–9. Capitate-sessile glands. **7.** Gland head with several celled secretory disc, secretory cavity, and bounding sheath. × 696. **8.** Gland, longitudinal section with secretory disc, short supporting axis, and disrupted secretory cavity. Druses are characteristic of subepidermal tissue. × 696. **9.** Mature gland with torn sheath and exposed eight-celled secretory disc. × 1,546.—Fig. 10 13. Capitate-stalked glands. **10.** Abscised gland head with 12–13 celled secretory disc. × 500. **11.** Longitudinal section of mature gland with gland head supported by tall multicellular stalk. Both epidermal and subepidermal tissue contribute to stalk formation. × 223. **12, 13.** Living gland viewed at two focus levels. Secretory product (arrow) is visible as spheres of different size within secretory cavity of gland head. × 325.


B
V
Se
T
14
SO
St
15
16
St
Se
Se
B
B
17
SP
BC
MS
18
19
20
21

the gland epidermal initial. The stalk consists of surface cells continuous with the bract mesophyll (Fig. 11).

The number and arrangement of secretory cells in the gland head is seen in a whole mount of an abscised head (Fig. 10). A faintly discernable inner circle of cells is related to walls of the underlying stipe layer which are out of the plane of focus. Fresh whole mounts of capitate-stalked glands viewed at two levels of focus (Fig. 12, 13) illustrate the spatial relationship of the secretory cell layer to the secretory product and surrounding sheath. The secretory product accumulates as distinct spherical bodies of varying size (Fig. 13) which can be liberated by rupture of gland heads in whole mount preparations.

The three gland types are not vascularized nor do they develop in close association to laticifers or vein endings.

Comparative morphogenesis of glandular hair types—Gland morphogenesis on developing bracts was studied primarily by SEM which enables one to determine from cell contour the position, size, and number of cells for a large gland sample. Young bracts 1–3 mm in length (Fig. 14) already possess numerous well developed bulbous and capitate-sessile glands. Younger bracts, less than 1 mm in length, were very difficult to isolate from the numerous other primordia of complex young inflorescences.

It is often not possible to distinguish immature bulbous glands from very young capitate-sessile or capitate-stalked glands until gland heads of the latter types develop beyond a 4-celled stage. Bulbous glands nearing maturity, however, may be readily identified by the presence of a secretory product or secretory cavity in their few-celled head.

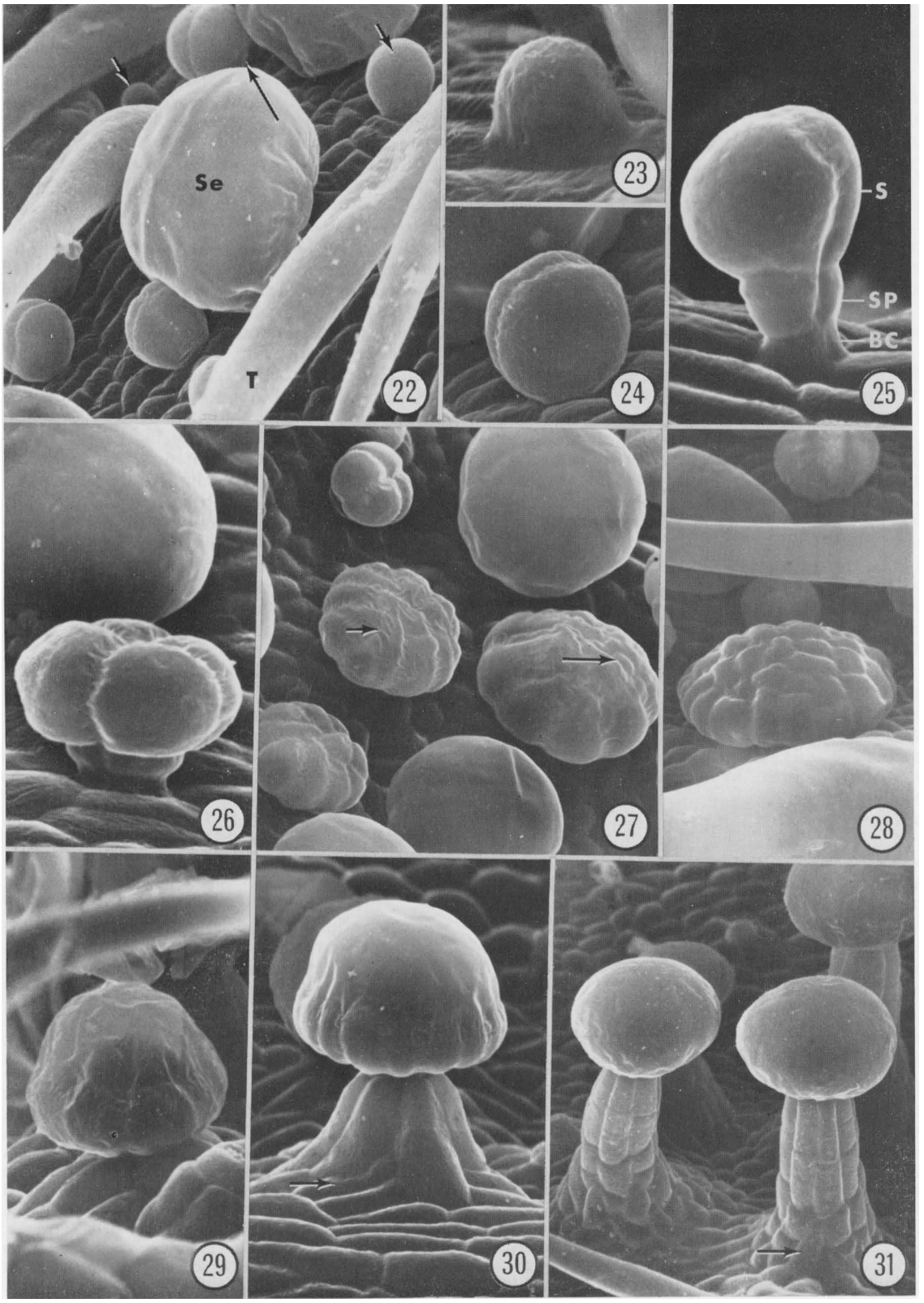
Capitate-sessile gland development can be observed from several intermediate stages of late maturing glands (Fig. 14, arrows). Cells of the secretory disc undergo considerable enlargement only after cell division is completed. This is followed by formation and enlargement of the secretory cavity as evidenced by a series of gland heads of increasing diameter.

Capitate-stalked glands, recognized by their immature multicellular stalks, are first found on vein ridges of medium aged 4–6 mm bracts which already bear well developed bulbous and capitate-sessile glands (Fig. 15). At this time, stalked glands are absent from other areas of the bract. Occasionally, under altered growth conditions, these immature stalked glands can be found at earlier stages of bract growth. In slightly older bracts, mature stalked glands line the vein ridges while immature stalked glands are found in interveinal regions (Fig. 16). On mature bracts, 8–10 mm long, capitate-stalked glands with tall multicellular stalks are scattered over most of the bract surface interspersed with the matured capitate-sessile and bulbous glands (Fig. 17). Capitate-stalked glands are usually absent or infrequent along the bract margins.

A comparison of gland number on young and mature bracts shows that capitate-sessile glands are initiated and mature early in bract development while the development and maturation of capitate-stalked glands occur later and coincide with the major period of bract growth and maturation (Table 1). The average number of capitate-stalked glands on mature bracts increased over 60 fold compared to those present on young bracts, whereas there was only a 0.1 fold increase for the capitate-sessile category. The total number of these glands on young as contrasted with mature bracts increased three times during bract growth from 2 to 8 mm in length.

Morphogenesis of capitate-stalked glands—Early stages of capitate-stalked gland development can be located by surveying those areas where the glands are known to appear in great abundance. Capitate-stalked gland initiation begins by a protrusion of individual epidermal cells (Fig. 22, short arrows, 23). The first division of the initial is anticlinal and bisects the young gland in the plane of the long axis of the bract (Fig. 22, 24). This division establishes a bilateral gland symmetry which is especially prominent in young stages and is maintained throughout further development. A periclinal division through the upper portion of the gland follows the longitudinal

Fig. 14–21.—Fig. 14–17. Distribution and types of glands on developing bracts. **14.** Young 2 mm long bract with abundant bulbous and capitate-sessile glands. Several late forming capitate-sessile glands are present (arrows). Young glands along vein ridge include incipient stages of capitate-stalked glands. × 247. **15.** Medium aged 4–6 mm long bract with first appearance of stalks on immature capitate-stalked glands located on vein ridge. × 378. **16.** Slightly older bract with mature capitate-stalked glands on vein ridge and development of immature stalked glands in interveinal regions. × 115. **17.** Old 8–10 mm bract with mature capitate-stalked glands uniformly distributed among earlier matured capitate-sessile and bulbous glands. × 104.—Fig. 18–21. Capitate-stalked gland abscission. **18.** Two abscission layers in auxiliary portion of gland at juncture of gland head and multicellular stalk (arrows). × 1,512. **19.** Gland head abscission at base cell layer. × 300. **20.** Capitate-stalked gland prior to stalk formation with gland head lost at base cell layer. × 753. **21.** Mature stalked gland stage after abscission of gland head at stipe cell layer. × 600. See p. 1025 for Key to Labeling.


Se
T
22
23
24
S
SP
BC
25
26
27
28
29
30
31

division (Fig. 22, long arrow). This division delimits an upper pair of cells, the secretory portion, that will give rise to the secretory cells of the head and a lower pair of cells, the auxiliary portion, which will give rise to the base and stipe cell layers.

A second periclinal division within this auxiliary portion delimits the base and stipe cell layers (Fig. 25). The pair of base cells embedded in the epidermis form the lowermost layer of the gland proper and do not undergo further cell division. However, the pair of stipe cells do undergo a further anticlinal division at right angles to the existing wall to form a four-celled layer which supports the gland head (Fig. 26). The stipe cells remain as a four-celled layer throughout further gland development.

Development of the gland head following the two-celled stage results from an anticlinal division at right angles to the existing wall producing a four-celled stage (Fig. 25). Occasionally, intermediary three-celled stages are found. The four cells of the head become flattened by radial enlargement (Fig. 26) and continue to divide anticlinally to produce a flattened disc of approximately 8 to 13 cells. Subsequently, division ceases and the disc cells enlarge nearly doubling the diameter of the gland head (Fig. 27, note three stages of successive enlargement).

Formation of the secretory cavity commences with the onset of secretory activity as evidenced by the progressive enlargement of the space above the secretory disc during the final stages of disc enlargement. Cavity formation becomes evident first as a slight wrinkling of the upper surface of the gland head (Fig. 27, short arrow) followed by loose folds and swellings of the surface in the central region of the head (Fig. 27, long arrow, 28) with concomitant loss of cellular contour in that area. Continued enlargement of the secretory space gives the gland head first a dome shape and then a more spherical shape (Fig. 29). Loosening of the sheath is delayed on the sides of the head where the surface outline of the underlying cells and vertical folds in the sheath remain visible (Fig. 29, 30).

TABLE 1. *Total number of sessile and stalked glands at stages in bract growth*[a]

Bract stage	Sample	Gland type		Total gland number, avg.
		Sessile[b]	Stalked	
Young, 2 mm	1	198	5	
	2	193	0	
	3	265	19	
	4	248	23	
	Avg.	226	12	238
Mature, 7–8 mm	5	296	804	
	6	291	842	
	7	185	589	
	Avg.	257	745	1,002

[a] Actual gland counts from SEM micrographs using plants flowering under natural photoperiods in greenhouse.

[b] This category includes all glands with heads larger than 30 μm diam or more than four secretory cells and those which lacked multicellular stalks.

When the gland head approaches its full size, it becomes elevated upon a multicellular stalk formed by the localized growth of surrounding epidermal cells (Fig. 30). At the onset of stalk growth, the radially arranged epidermal cells surrounding the gland (Fig. 20, 29) elongate vertically raising the gland proper (base, stipe, and secretory cells) above the bract surface. In addition, adjacent epidermal cells also contribute to the structure of the multicellular stalk as seen in younger (Fig. 30, arrow) and slightly older (Fig. 31, arrow) stages of stalk development. Epidermal cells in the upper regions of the multicellular stalk frequently undergo transverse divisions. The relative contribution of cell elongation and cell division to growth of the multicellular stalk may vary, resulting in stalks of different height and cell number on mature bracts (Fig. 17). The contribution of subepidermal layers to stalk growth cannot be determined by surface observation, although its extent is evident from mature glands viewed in longitudinal section (Fig. 11).

←

Fig. 22–31. Morphogenesis of the capitate-stalked gland type. **22.** Gland initials (short arrows) and subsequent two-celled stage produced by anticlinal division. A second periclinal division (long arrow), delimits an upper secretory portion and lower auxiliary portion. × 967. **23.** Gland initial stage. × 2,247. **24.** Two-celled gland stage. × 2,043. **25.** Young gland following periclinal division in lower half of auxiliary portion producing basal and stipe cell layers. × 1,387. **26.** Formation of flattened, four-celled gland head and four-celled stipe layer. Basal cell layer remains two-celled. × 1,904. **27.** Stages of increasing cell size and number of secretory discs (arrows). × 774. **28.** Formation of secretory cavity with onset of gland secretory activity. × 587. **29.** Ballooning of sheath containing the enlarging resin filled secretory cavity. The radially arranged epidermal cells surrounding gland initiate formation of multicellular stalk. × 872. **30.** As head approaches full size, epidermal cells that contact the gland proper (base, stipe, and secretory cells) elongate raising it above the bract surface. × 724. **31.** Mature capitate-stalked glands. Stalk growth results from continued elongation and division of stalk epidermal cells. Additionally, epidermal cells more distal to those initially contacting the gland proper contribute to stalk development (arrows). × 253. See p. 1025 for Key to Labeling.

Mature capitate-stalked glands, unlike bulbous or capitate-sessile types, possess a dehiscence mechanism whereby the gland head separates from the multicellular stalk when physically disrupted. This mechanism is formed by the development of an abscission region in both the base and stipe cell layers (Fig. 18, arrows). Abscission at the base cell layer (Fig. 19, 20) leaves the outline of the pair of base cells in relief whereas abscission at the stipe cell layer (Fig. 21) leaves the quadrant of stipe cells in relief.

DISCUSSION—This study of gland morphogenesis clarifies more fully the types and relationships between the glands present on bracts and provides initial information on the pattern of gland development in *Cannabis*. We consider the glandular system to consist of three gland types distinguishable on the bases of morphology, development, and physiology.

Morphologically, bulbous glands are easily separated from the capitate-sessile and capitate-stalked types based on their diminutive size and the few-celled condition of the mature gland head. The main feature that separates capitate-stalked from capitate-sessile glands is the production of the multicellular stalk. At first consideration, the stalk does not appear to be part of the gland in that it is not derived from the gland initial. If one would take this position, a non-glandular nature of the stalk would be emphasized and it then could be termed a pseudostalk (Dayanandan and Kaufman, 1976) or pseudo-stipe (Uphof, 1962) and the distinction between capitate-sessile and capitate-stalked glandular types would be minimized. In contrast, when the capitate-stalked gland is viewed as a distinct gland type, several productive concepts emerge. It is evident that the development of the multicellular stalk has an interdependent association with the gland. The gland exerts some control upon development of its multicellular stalk either by triggering or maintaining its growth because stalks are not observed to form in the absence of the gland head.

Differences in time of gland initiation and maturation also indicate a distinctness for gland types. Bulbous and capitate-sessile glands arise and mature in early bract growth. Capitate-stalked glands arise somewhat later and form first on the vein ridges and subsequently in interveinal regions of the bract. There is no indication that stalk formation is triggered on the sessile form for, if it were, the sessile forms already present on the interveinal regions of young bracts should be the first to develop stalks. If the early formed sessile glands mature into stalked glands, they would do so only after a delayed period, a condition not observed in the pattern of capitate-stalked gland development. Counts of capitate-sessile and capitate-stalked glands from young and mature bracts support the distinctness of gland types. These data indicate that capitate-sessile gland production does cease early in bract growth and that the number of these glands remains quite constant during the ensuing period of bract growth. Similar findings were determined by Turner, Hemphill, and Mahlberg (1977) for drug and non-drug lines of other varieties of *Cannabis*.

Initiation of capitate-stalked glands occurs by an anticlinal division of a single epidermal initial. Rauter (1872), in a study of the capitate and peltate gland types that occur in the related genus, *Humulus*, reported that the glands are initiated by an anticlinal division of a single gland initial. Although a bulbous gland type was not found in *Humulus*, development of the capitate types is similar to immature stages of gland development in *Cannabis*.

Glands of *Cannabis* have been reported to arise from enlargement and division of a single epidermal initial (Briosi and Tognini, 1894; Mohan Ram and Nath, 1964; Dayanandan and Kaufman, 1976), although often no distinction could be made regarding the type of gland that an initial would form. Mohan Ram and Nath (1964), in their work on *Cannabis* floral anatomy, described gland initiation as occurring by enlargement of an epidermal cell that then underwent a perclinal (only rarely anticlinal) division. Dayanandan and Kaufman (1976), who recognized only capitate and bulbous glands, diagrammed the early development of glands from a staminate plant as beginning with a periclinal division of the gland initial. These descriptions of a periclinal division initiating gland development stand in contrast to our findings which have been substantiated by studies on the ultrastructure of gland development (Hammond and Mahlberg, in preparation). Descriptions of a periclinal division in gland initiation may have pertained to early development of a bulbous type gland. Certainly in a bulbous gland that possesses a single base, stipe, and stalk cell, all divisions had to be perclinal. Our description of initiation of capitate-stalked glands by an anticlinal division, therefore, may reflect a pattern associated with a different gland type and may serve to further characterize this gland type.

This analysis of gland morphogenesis, with few exceptions, incorporates the range of morphological gland structures which have been described for *Cannabis*. One variation in gland structure not observed in our bract material is the gland described by Fairbairn (1972) which lacked internal cellular structure as well as a supporting stipe. This gland may be identical to the "disk-shaped glandular hair type 1" which Shimomura et al. (1967) described as being distinct from other sessile glands in having a secretory disc with few cells and indistinct walls.

The restricted localization of capitate-stalked glands on flowering regions of pistillate plants, especially bracts, suggests that a physiological state of this region may interact with glands to regulate their development. The fact that capitate-stalked glands arise first over bract veins or are characteristically restricted to veinal regions when found in vegetative areas further supports this view. Interestingly, one would predict that in the absence of this proper physiological state, such as in staminate plants or vegetative regions of pistillate plants, capitate-stalked glands might be present, but not distinguishable from capitate-sessile glands because their development could be arrested at an immature stage. Reports of "new" types of glands may reflect these altered developmental stages of capitate-stalked glands.

Capitate-stalked glands are of particular evolutionary interest in consideration of their present structural and functional roles. The evolution of this gland type may have been the result of selection pressure for the added advantage of a stratified glandular system. Such a glandular covering on bracts would maximize any protective advantage afforded to the developing fruit and seed against desiccation or herbivory, although functional roles have not been well established. The capitate-stalked gland type, thus, may have been derived from the simpler capitate-sessile type by the relatively non-disruptive means of superimposing a secondary developmental phase of epidermal cell growth upon existing glandular structures. Comparisons of functional roles of capitate-sessile to capitate-stalked glands in their biogenesis or accumulation of the marihuana hallucinogen, tetrahydrocannabinol, represents a potential area of investigation.

Consideration of *Cannabis* glands as three distinct types provides a logical framework for interpreting the structural and evolutionary complexities of this glandular system as well as for predicting several promising areas of future experimental research on gland structure and function.

LITERATURE CITED

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

BRIOSI, G., AND F. TOGNINI. 1894. Intorno alla anatomia della canapa (*Cannabis sativa* L.) Parte prima: Organi sessuali. Atti Ist. Bot. Pavia, Ser. 2, 3: 91–209.

DAYANANDAN, P., AND P. B. KAUFMAN. 1976. Trichomes of *Cannabis sativa* L. (Cannabaceae). Amer. J. Bot. 63: 578–591.

DE BARY, A. 1884. Comparative anatomy of the vegetative organs of the phanerogams and ferns. Translated by F. O. Bower and D. H. Scott. Clarendon Press, Oxford.

DE PASQUALE, A., G. TUMINO, AND R. C. DE PASQUALE. 1974. Micromorphology of the epidermic surfaces of female plants of *Cannabis sativa* L. Bull. Narcotics 26: 27–40.

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

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.

HANSTEIN, J. 1868. Über die Organe der Harz und Schleim-Absonderung in den Laubknospen. Bot. Zeit. 26: 697–787.

LEDBETTER, M. C., AND A. D. KRIKORIAN. 1975. Trichomes of *Cannabis sativa* as viewed with scanning electron microscope. Phytomorphology 25: 166–176.

LEVIN, D. A. 1973. The role of trichomes in plant defense. Q. Rev. Biol. 48: 3–15.

LÜTTGE, U. 1971. Structure and function of plant glands. Annu. Rev. Plant Physiol. 22: 23–44.

MOHAN RAM, H. Y., AND R. NATH. 1964. The morphology and embryology of *Cannabis sativa* Linn. Phytomorphology 14: 414–429.

RAUTER, J. 1872. Zur Entwicklungsgeshichte einiger Trichomgebilde. Akad. Wiss. Wien. Math. Naturwiss. Kl. Denkschr. 31: 1–48.

SHIMOMURA, H., M. SHIGEHIRO, E. KURIYAMA, AND M. FUJITA. 1967. Studies on *Cannabis*. I. Microscopical characters of their internal morphology and spodogram. Annu. Rep. Tokyo Coll. Pharm. 17: 232–237.

SMALL, E., AND A. CRONQUIST. 1976. A practical and natural taxonomy for *Cannabis*. Taxon 25: 405–435.

———, P. Y. JUI, AND L. P. LEFKOVITCH. 1976. A numerical taxonomic analysis of *Cannabis* with special reference to species delimitation. Syst. Bot. 1: 67–84.

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

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: 689–695.

UNGER, F. 1856. Grundlinien der Anatomie und Physiologie der Pflanzen. Bramüller, Wien.

UPHOF, J. C. TH. 1962. Plant hairs, p. 1–206. *In* W. Zimmermann and P. G. Ozenda [ed.], Encyclopedia of plant anatomy, vol. 4, part 5. Gebrüder Borntraeger, Berlin.