

ANATOMICAL STUDIES IN THE GENUS *DIGITALIS*

PART II. THE ANATOMY OF THE INFLORESCENCE OF *D. lanata* L.

BY P. S. COWLEY AND J. M. ROWSON

From the School of Pharmacy, Brighton Technical College, and The Pharmacy Department, Nigerian College of Technology, Ibadan

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The morphology and detailed anatomy of the inflorescence of *Digitalis lanata* have been described. The diagnostic characters which are the most valuable in identifying the inflorescence in admixture with the leaf are the abundance of glandular trichomes; the pollen grains; the sclerenchymatous fibres and lignified pith of the pedicel and stem; also the lignified cells of the anther, fruit wall and seed coat. Those characters which may be used to distinguish the inflorescence from that of *D. purpurea* are noted.

WE have previously described the morphology and detailed anatomy of the inflorescence of *Digitalis purpurea* L.¹ This communication describes the morphology and anatomical structure of *D. lanata* L.

The morphological description is complementary to the descriptions already made²⁻⁶.

Material

The inflorescences used were from several clones kindly provided by the Royal Botanical Gardens, Kew, and by the Chelsea Physic Gardens. The mature flowers possessed those characters of floral morphology accepted as typical of *Digitalis lanata* L.

Experimental Methods

These were the same as described previously¹.

GROSS MORPHOLOGY

In the mature flower the calyx consists of five deeply partite sepals. The posterior and posterior-lateral sepals are lanceolate, about 8 mm. long and 2.5 mm. broad; the anterior-lateral sepals are ovate, about 8 mm. long and 3.5 mm. broad (Fig. 1, A). The gamopetalous corolla tube is about 9 mm. long, 7 mm. wide at the distal end and 2.5 mm. wide at the proximal end. Each of the five net-veined petal lobes has a recurved margin. The anterior petal is about 15 mm. long, its large free lobe bends upwards and as a flap almost closes the corolla tube (Fig. 3, A).

The androecium consists of four didynamous stamens. The filaments are slightly pubescent, curved and about 1 mm. wide. The variation in length of the adherent portion is similar to that described for *D. purpurea*.¹ Anther lobes are slightly pubescent, about 2.5 mm. long and 1 mm. wide (Fig. 4, A). Dehiscence is introrse. The syncarpous gynaecium is about 4 mm. long and 2 mm. wide at the base. The nectary is a slightly undulating ring of tissue at the base of the ovary (Fig. 5, A). The style,

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firm, erect, pubescent except near the stigma, arises from the apex of the ovary and is 3–4 mm. long and 0.5 mm. wide. The stigma, terminal and glabrous is formed of two small lobes (Fig. 5, B).

The brownish-green fruit with its erect, persistent calyx, is about 10 mm. long and 4 mm. wide at the base. Dehiscence is septicial (Fig. 6, A and B).

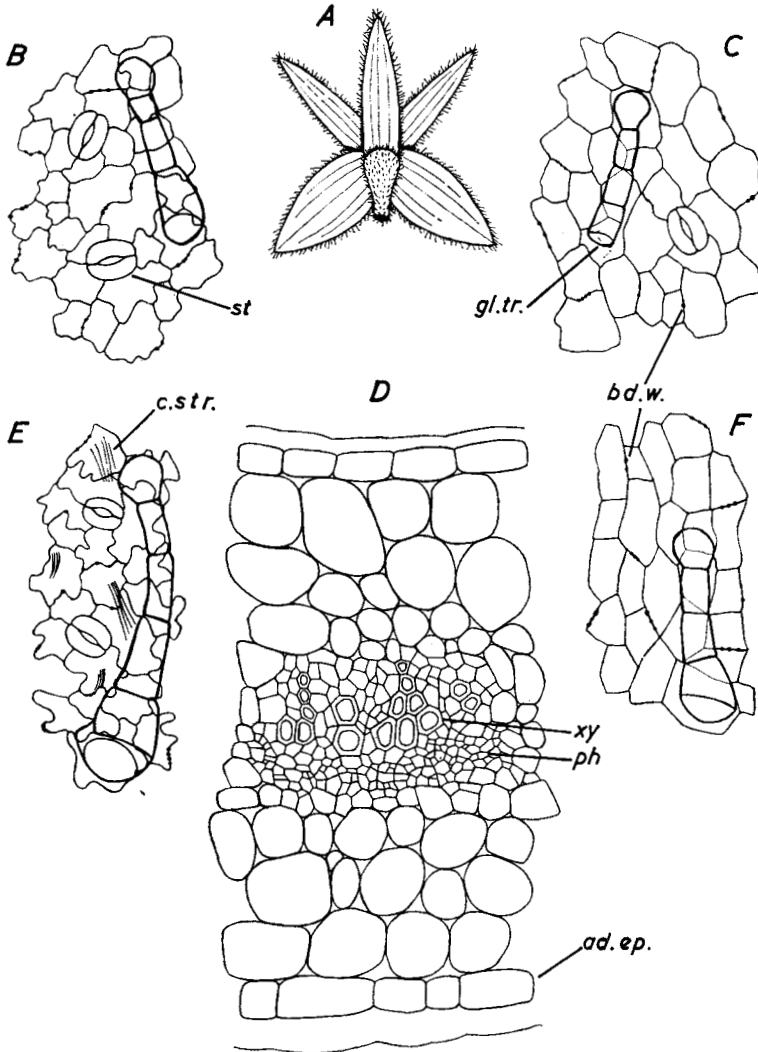


FIG. 1. *Digitalis lanata* L. Calyx. A, Ventral view of Calyx $\times 2$. B, Abaxial epidermal cells from apical and central regions. C, Abaxial epidermal cells from basal region, both $\times 170$. D, Transverse section through a main vein $\times 350$. E, Adaxial epidermal cells from apical and central regions. F, Adaxial epidermal cells from basal region, both $\times 170$. ad. ep., adaxial epidermis; bd.w., beaded walls of epidermal cells; c.str., cuticular striations; gl.tr., glandular trichome; ph, phloem; st, stigma; xy, xylem.

The numerous reddish-brown sub-conical seeds are about 1.5 mm. long and 0.75 mm. broad with at least one obvious groove indicating the line of the raphe. They vary much in shape from trapezoid to nearly ovoid. A small circular scar at one end of the groove marks the position of the hilum (Fig. 2, B).

HISTOLOGY

Calyx. The abaxial surface is covered by a thick, smooth cuticle. The epidermal cells at the base are polygonal with straight or slightly

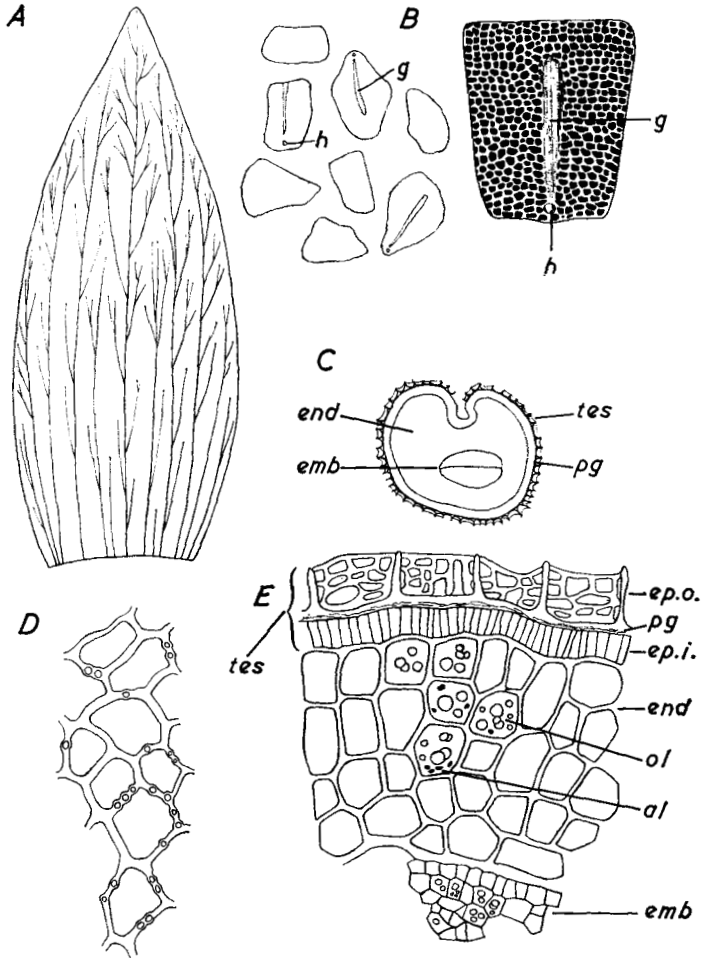


FIG. 2. *Digitalis lanata* L. Calyx and seed. A, Sepal, plan of venation $\times 7$. B, Outline of seeds showing variation in shape $\times 8$, also one seed $\times 16$ showing macroscopical detail. C, Tissue plan of transverse section of seed $\times 16$. D, Testa in surface view $\times 170$. E, Transverse section of seed $\times 170$. emb, embryo; end, endosperm; ep. i., inner epidermis; ep. o., outer epidermis; g, groove; h, hilum; ol, oil globules; al, aleurone grains; pg, pigment; tes, testa.

wavy beaded walls, *L and T⁷ 16-30-40-60 μ (Fig. 1, C). Over the remainder of the surface the epidermal cells have similar measurements, their walls are beaded, wavy or very wavy (Fig. 1, B). There is no elongation of epidermal cells over the veins. Anomocytic⁸ stomata are present on this surface (Fig. 1, B and C), they are 32-38-46 μ long, 20-26-36 μ wide. The stomatal index is not more than 1 in the basal region and up to 7 with a mean of 4 over the rest of the surface. Abundant trichomes, mainly glandular, are present. They have a unicellular head and a unicellular or multicellular pedicel (Fig. 1, B and C), on the edges of the sepals they occur in numbers varying from 27-36-58-64 per mm., they are 200 μ -1.2 mm.-1.8 mm. long, 28-52-84 μ wide at the base, with 3-6-8 cells per pedicel. In the interneural areas there are 54-72-90-114 per sq. mm., they are 98-350-400-1400 μ long, 28-42-56-98 μ wide at the base, with 1-3-6 cells per trichome. Non-glandular trichomes with a smooth cuticle and an acute apical cell, occur only on the margin of the sepals near their apex. They are 240-840-1380 μ long 24-36-60 μ wide at the base, with 2-4-7 cells per trichome.

On the adaxial surface the epidermal cells are similar except that the cuticle is somewhat thinner and is striated in the central and apical regions (Fig. 1, D and E). Stomata also are similar, but their distribution differs, being absent in the basal region and rare over the remainder of the surface, where the stomatal index is about 3. Glandular trichomes only are present, 48-120-168-300 μ long, 12-24-48 μ wide at the base, 1-3-6 cells per pedicel. Their number per sq. mm. varies from 50-110, being least in the basal region.

The interneural mesophyll is a loose tissue of about 10 rows of undifferentiated round to ovoid parenchymatous cells containing chloroplasts with associated starch grains (Fig. 1, D). In each sepal the vascular tissue consists of about five main veins, with secondary and tertiary veinlets in the central and apical regions (Fig. 2, A). Each of these main collateral strands consists of a small roughly crescent-shaped arc of xylem vessels, about 14-30 μ in diameter, arranged in small groups or files. Medullary ray cells separate the groups or files. Adjacent to the arc of xylem is a narrow band of phloem consisting of sieve tubes 4-10 μ in diameter, with companion cells and phloem parenchyma (Fig. 1, D). Starch sheath and sclerenchymatous fibres were not present in those sepals examined. The veinlets consist of a small group of polygonal tracheids 3-6 μ in diameter, with a small amount of indistinct phloem tissue.

Corolla. The abaxial surface is covered by a thin, smooth cuticle. Those epidermal cells around the base of the corolla tube and extending about half way along the posterior petals are polygonal, straight-walled cells, elongated in the direction of the longitudinal axis of the petals.

* In recording measurements the letters L, T and R, have reference to the longitudinal, tangential and radial directions respectively, of the plant member in question. In cases where orientation of the subject relative to the plant axis is absent, values for L and T are combined. In any set of measurements a number in bold type refers to the mean. Where most commonly occurring sizes do not appear, by inspection, to be similar to the mean, two numbers in bold type are given. These refer to the most commonly occurring size range.

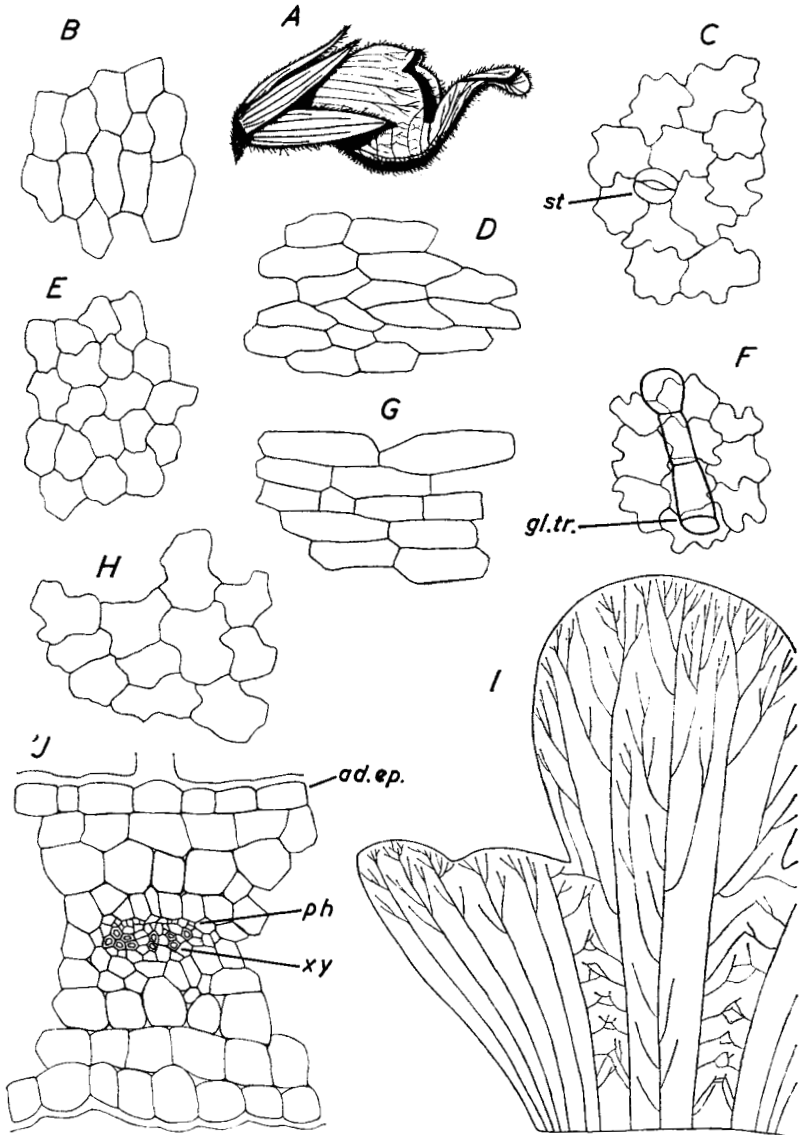


FIG. 3. *Digitalis lanata* L. Corolla. A, lateral view of corolla $\times 2$. B, Abaxial epidermal cells from central region. C, Abaxial epidermal cells from distal region. D, Abaxial epidermal cells from proximal and posterior central region. E, Adaxial epidermal cells from central region. F, Adaxial epidermal cells from distal region. G, Adaxial epidermal cells from posterior central region. H, Adaxial epidermal cells from proximal region, all $\times 170$. I, Corolla, plan of venation $\times 4$. J, Transverse section through vascular bundle of corolla $\times 170$. ad. ep., adaxial epidermis; gl. tr., glandular trichome; ph, phloem; st, stoma; xy, xylem.

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They measure L, 40-78-120 μ , T, 12-20-30 μ , R, 16-20-28 μ (Fig. 3, D). Over the rest of the surface the cells are nearly isodiametric with wavy walls, very wavy on the free lobes (Fig. 3, B and C). They measure L and T, 24-35-64-90 μ , R, as for cells at the base of the petal. Stomata similar to those on the calyx are found on this surface (Fig. 3, C), although they are absent from the basal region and very rare on the free lobe of the anterior petal. Apart from these areas the stomatal index varies from 5-10-25-32. Trichomes similar to those found on the calyx are present, the glandular type predominating. These are more numerous in the distal region, especially on the free lobe of the anterior petal. There are 3-11 per sq. mm., they are 84-308-560 μ long, 14-42-60 μ wide at the base, with 2-3-5 cells per pedicel. Non-glandular trichomes are present on the margin and extreme distal area of the anterior petal. There are 2-13 per mm. of margin and 0.3-1 per sq. mm. of interneural area. They are 250-434-700 μ long, 28-42-60 μ wide at the base, with 2-5-7 cells per trichome.

On the adaxial surface the cuticle is smooth. The epidermal cells are polygonal and nearly isodiametric in the apical region becoming increasingly elongated in part of the central region; their outer walls are domeshaped, (Fig. 3, E, F, G and H). The elongated cells from the posterior part of the central region measure L, 30-68-100 μ , T, 20-26-40 μ , the nearly isodiametric cells over the rest of the surface measure L and T, 16-24-34-50 μ . R for all these cells is 16-32-40 μ . Glandular trichomes are present on the anterior petal in numbers from 3-9 per sq. mm. On the lateral petals they are present only on the central and basal regions in numbers from 1-6 per sq. mm. On the posterior petals they are absent or rare. They measure 56-224-460 μ long, 14-28-70 μ wide at the base, with 1-4 cells per pedicel. Non-glandular trichomes are present in the apical region only in numbers from 0.3-3 trichomes per sq. mm. They are 210-400-700 μ long, 28-40-70 μ wide at the base, with 1-6 cells per trichome.

The mesophyll is similar to that of the calyx save for the absence of chloroplasts with starch grains and the presence of anthocyanin and flavone pigments and smaller intercellular air spaces (Fig. 3, J). Twelve to 18 main veins are found in the corolla together with secondary and tertiary veinlets which unite the main veins. These veinlets are particularly numerous in the areas of fusion between the anterior and lateral petals (Fig. 3, I). Veins and veinlets are similar in structure except for the size and number of the elements. The xylem vessels, 4-10 μ in diameter, with polygonal, lignocellulosic walls having spiral and annular thickening, are arranged in groups or files separated by medullary ray cells. The phloem tissue contains sieve tubes 3-6 μ in diameter, companion cells and phloem parenchyma (Fig. 3, J).

Androecium. The filament is covered by a thin, smooth cuticle. The thin walled, polygonal epidermal cells are elongated, the elongation is greatest in the central region where they measure L, 60-96-170 μ , T, 12-18-22 μ . In the apical and basal regions, L, 30-42-50 μ , T, 14-18-24 μ and L, 60-86-110 μ , T, 16-28-36 μ respectively. Throughout R

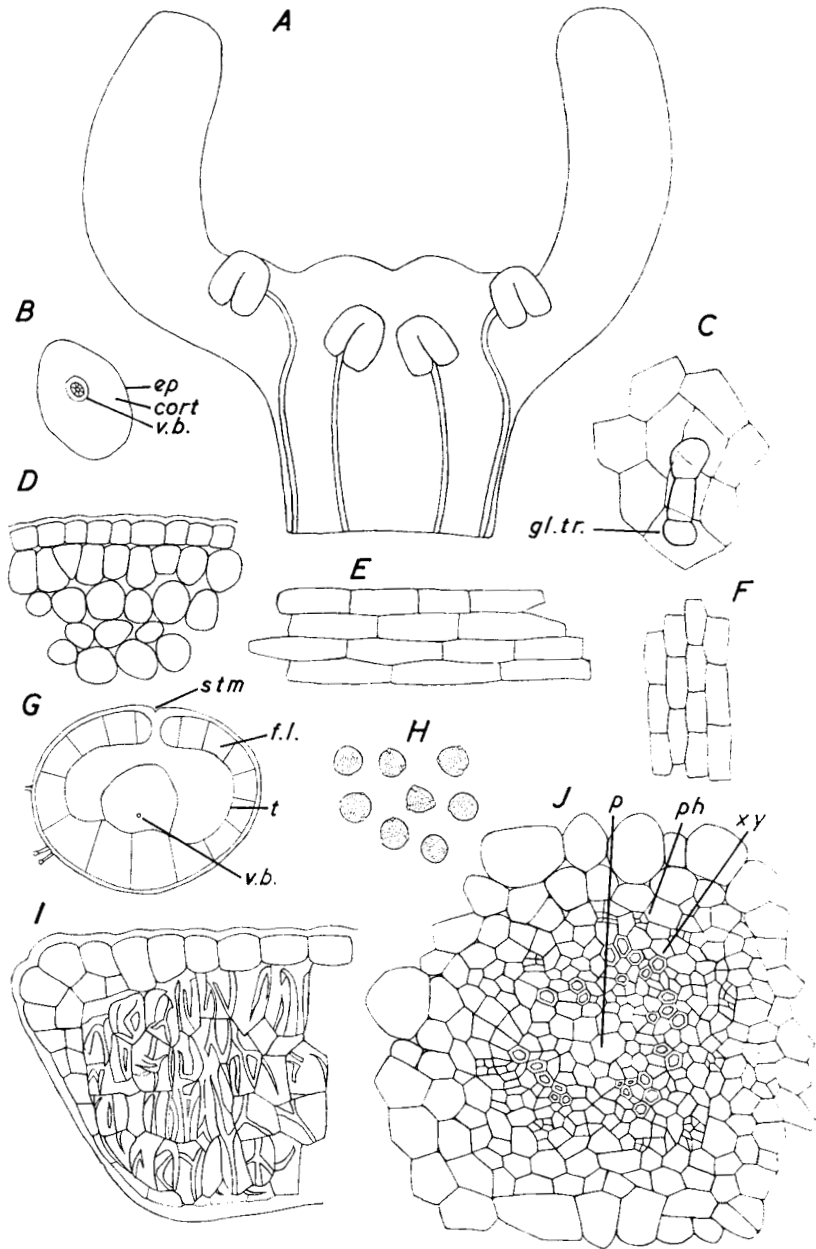


FIG. 4. *Digitalis lanata* L. Androecium. A, Plan of corolla to show position of stamens $\times 5$. B, Tissue plan of transverse section of filament $\times 25$. C, Epidermal cells from anther lobes. D, Transverse section of filament, epidermis and cortex. E, Epidermal cells from filament. F, Epidermal cells from filament near anther, all $\times 170$. G, Tissue plan of transverse section of anther before dehiscence $\times 30$. H, Pollen grains. I, Transverse section of anther wall at stomium, both $\times 170$. J, Transverse section of vascular strand of filament $\times 350$. cort, cortex; ep, epidermis; f.l., fibrous layer; gl. tr., glandular trichome; p, pith; ph, phloem; stm, stomium; v.b. vascular bundle; t, tapetum; xy, xylem.

measures 16–20 μ (Fig. 4, D, E and F). Stomata were not found on the filaments. Glandular trichomes are present on the free portion of the filament in numbers from 8–31 per filament. They measure 70–168–300 μ long, 14–28–56 μ wide at the base, with 1–3 cells per pedicel.

The cortex consists of a loose tissue of about 5–18 rows of rounded or irregularly rounded, thin walled parenchymatous cells, with numerous intercellular air spaces, no cell inclusions were observed (Fig. 4, D). Embedded in the cortex is the slightly eccentric vascular strand. It consists of a small central pith surrounded by a discontinuous ring of polygonal, lignified xylem vessels 4–8 μ in diameter, with spiral and annular thickening. Around the xylem are groups of phloem with sieve tubes 3.5 μ in diameter (Fig. 4, J).

The anther lobes are covered by a thin cuticle. The epidermal cells are polygonal with slightly wavy walls (Fig. 4, C), L and T, 28–38–52–60 μ , R, 18–24–30 μ . Beneath the epidermis there are about five rows of nearly isodiametric cells with ligno-cellulosic thickening in spiral and annular bands (Fig. 4, G and I). They measure L and T, 16–26–34–50 μ , R, 20–32–48–60 μ . Remains of the collapsed tapetum are visible within this fibrous layer. Stomata are absent from the anther lobes. There are about 70 glandular trichomes on each lobe, 70–110–170 μ long, 14–28 μ wide, with 2–4 cells per pedicel (Fig. 4, C).

The pollen grains (Fig. 4, H), are subspherical, 20–24–28 μ in diameter, with three germinal pores. The intine is smooth, the exine very finely pitted. Starch and oil were not found in the grains examined.

Gynaecium. The ovary is covered by a thin smooth cuticle. The polygonal epidermal cells with straight walls measure L and T, 14–18–24–32 μ , R, 15–20–30 μ (Fig. 5, E). Stomata occur, length 18–24–28 μ , breadth 20–22–26 μ . Stomatal index varies up to 0.5. Glandular trichomes only occur, similar to those on the calyx, 84–250–430–980 μ long, the longest being near the apex of the gynaecium, 14–35–70 μ wide at the base, with 2–3–4–7 cells per pedicel. There are 0.3–1–2 trichomes per sq. mm. (Fig. 5, C, E and J). The cells of the inner epidermis (Fig. 5, F) are thin, straight walled and elongated at right angles to the longitudinal axis of the ovary, they measure L, 40–46–54 μ , T, 4–8 μ , R, 8–10–14 μ . Trichomes and stomata were not found on this inner surface.

The mesophyll is formed of polygonal cells with thin straight walls. They contain chloroplasts with associated small, round starch grains (Fig. 5, J). About 30 vascular strands are embedded in this mesophyll, the polygonal, lignified vessels, 4–8 μ in diameter, have spiral and annular thickening. The phloem is composed of very small elements. The placenta is formed of rounded cells with numerous intercellular air spaces (Fig. 5, I). About 10 vascular strands, similar to those in the mesophyll supply the placenta. Numerous ovules are borne on the placenta (Fig. 5, C).

The style is covered by a thin smooth cuticle. The polygonal, elongated, thin, straight walled epidermal cells measure L, 30–46–68 μ , T, 8–16–28 μ , R, 10–12–15 μ (Fig. 5, G). The cortex consists of round cells in which are embedded, opposite to each other and near the epidermis, two vascular

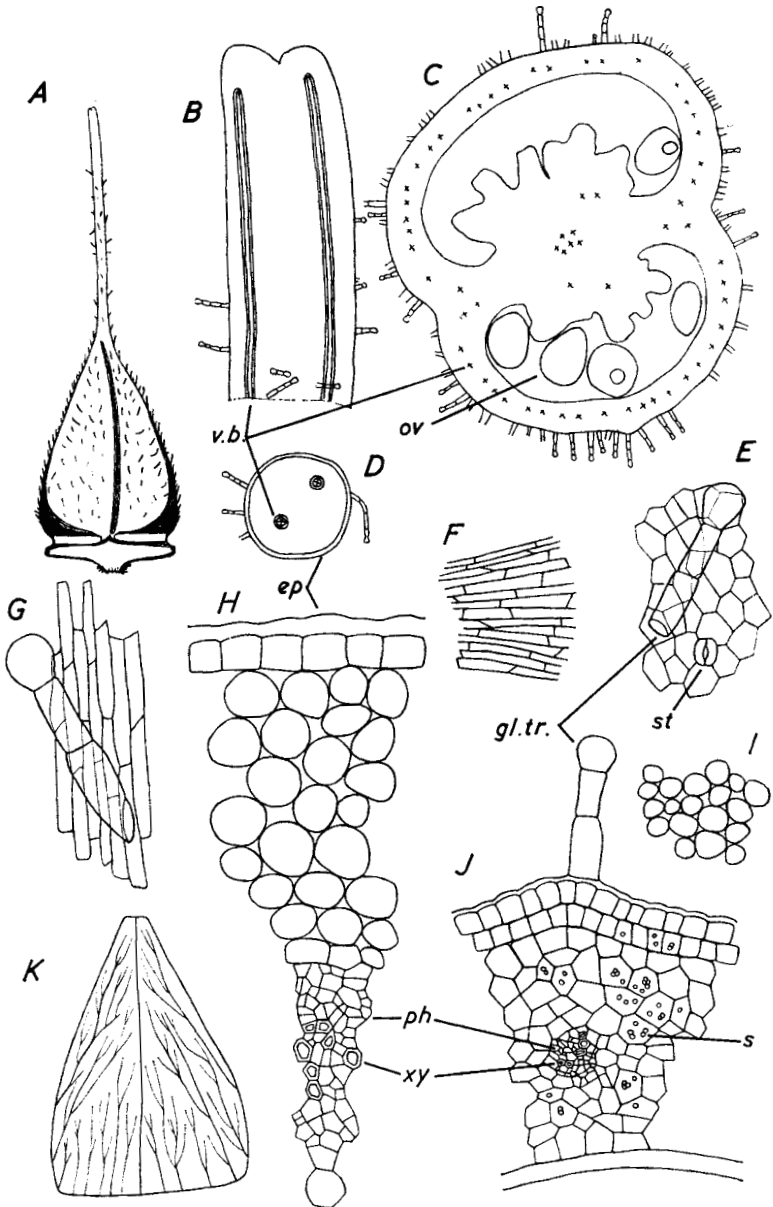


FIG. 5. *Digitalis lanata* L. Gynaecium. A, Gynaecium $\times 5$. B, Stigma and part of style with vascular strands $\times 17$. C, Transverse section of ovary $\times 17$. D, Transverse section of style $\times 17$. E, Outer epidermal cells from ovary wall. F, Inner epidermal cells from ovary wall. G, Epidermal cells from style, all $\times 170$. H, Transverse section of style through vascular strand $\times 350$. I, cells of placenta. J, Transverse section of ovary wall, both $\times 170$. K, Part of ovary wall, plan of venation $\times 7$. ep, epidermis; gl. tr., glandular trichome; ov, ovule; ph, phloem; st, stoma; v.b., vascular bundle; xy, xylem; s, starch.

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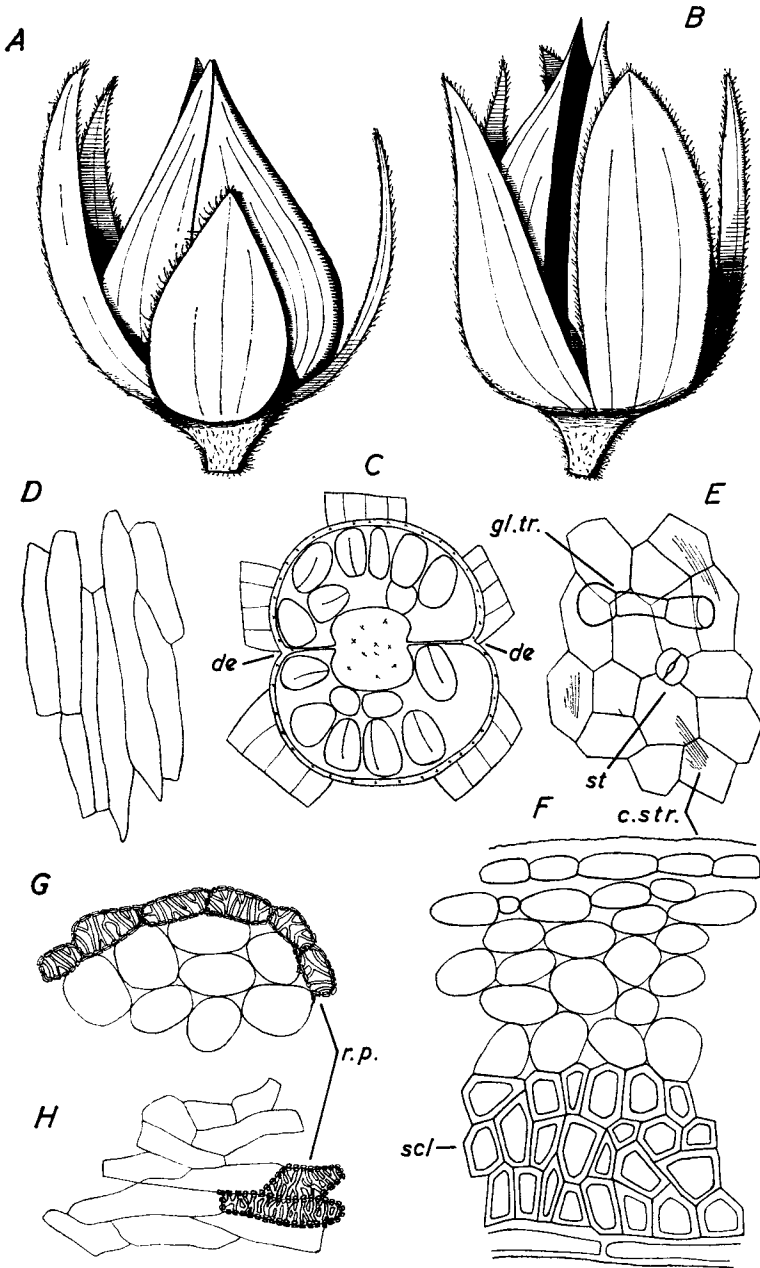


FIG. 6. *Digitalis lanata* L. Fruit. A, Fruit. B, Fruit after dehiscence. C, Transverse section of fruit, all $\times 5$. D, Inner epidermal cells of fruit wall. E, Outer epidermal cells of fruit wall. F, Transverse section of placenta. G, Transverse section of placenta. H, Covering cells of placenta in surface view, all $\times 170$. c.str., cuticular striations; de, dehiscence lines; gl. tr., glandular trichome; scl, sclerenchyma; st, stoma; r.p., reticulate parenchyma.

strands (Fig. 5, B and D). Each strand (Fig. 5, H), consists of a ring of lignified, polygonal xylem vessels, 4–10 μ in diameter, surrounded by a ring of very small celled phloem. The two strands supply the two lobes of the parenchymatous stigma (Fig. 5, B). Glandular trichomes occur on the style, except near the stigma (Fig. 5, B). There are 160–230 per style, 140–280–630 μ long, 28–40–70 μ wide at the base, with 2–3–5 cells per pedicel.

Fruit. The outer surface is covered by a thick cuticle, sometimes striated in the central and apical regions. The straight walled polygonal epidermal cells measure L and T, 24–28–60–90 μ , R, 12–16–20 μ (Fig. 6, E). Stomata similar to those on the ovary are present. Glandular trichomes only occur, 2–4 per sq. mm., 112–250–560 μ long, 14–40–56 μ wide at the base, with 2–3–5 cells per pedicel. The cells of the inner epidermis are similar to those of the ovary except that they are larger (Fig. 6, D). Trichomes and stomata are absent from this surface.

The mesophyll is formed of about 10 rows of cells. About 4 rows adjacent to the endocarp are sclerenchymatous, the remainder parenchymatous. These latter consist of a fairly loose tissue of round or ovoid cells containing some chloroplasts. The sclerenchymatous cells have thick stratified walls without pits (Fig. 6, F), they measure L and T, 22–26–54–70 μ , R, 14–30–50 μ . The vascular strands are similar to those in the ovary wall. The placenta has become covered with reticulate parenchymatous cells (Fig. 6, G and H). At the fruit stage the septum is bounded on both sides by the inner epidermis and sclerenchymatous layer (Fig. 6, C). The dehiscence is septicidal, splitting occurs in the central parenchyma.

Seed. The epidermal cells of the testa are lignified, reticulately thickened on the anticlinal walls, nearly isodiametric cells with the outer wall collapsed (Fig. 2, C, D, and E), L and T, 34–46–66–120 μ , R, 30–40–50 μ . The reddish-brown collapsed cells beneath the epidermis form a pigment layer. Beneath these there is a single row of palisade-like cells which is the inner epidermis of the testa. The endosperm consists of straight walled polygonal cells containing oil and protein. The central dicotyledenous embryo consists of cells similar to the endosperm cells but smaller and with thinner walls, they also contain oil and protein (Fig. 2, E).

Pedicel. The surface is covered by a thick smooth cuticle. The polygonal, elongated epidermal cells have thickened walls (Fig. 7, F), L, 36–60–80 μ , T, 12–16–22 μ , R, 7–10–14 μ . Stomata similar to those on the calyx are present, Stomatal Index varies from 0–3–6. Glandular trichomes only occur, 28–470–840 μ long, 28–60–110 μ wide at the base, with 2–4–7 cells per pedicel, there are 16–20–25 per sq. mm.

The cortex consists of about 9 rows of cells, the outer 3 of collenchyma, the rest parenchyma (Fig. 7, D). Within this cortex there is a complete band of about 6 rows of sclerenchymatous fibres, 8–26 μ in diameter and about 840 μ long, with slit-like pits in their walls (Fig. 7, D and G). These fibres surround a narrow band of phloem tissue with thin walled sieve tubes 8–12 μ in diameter. Cambial tissue is not distinct. The

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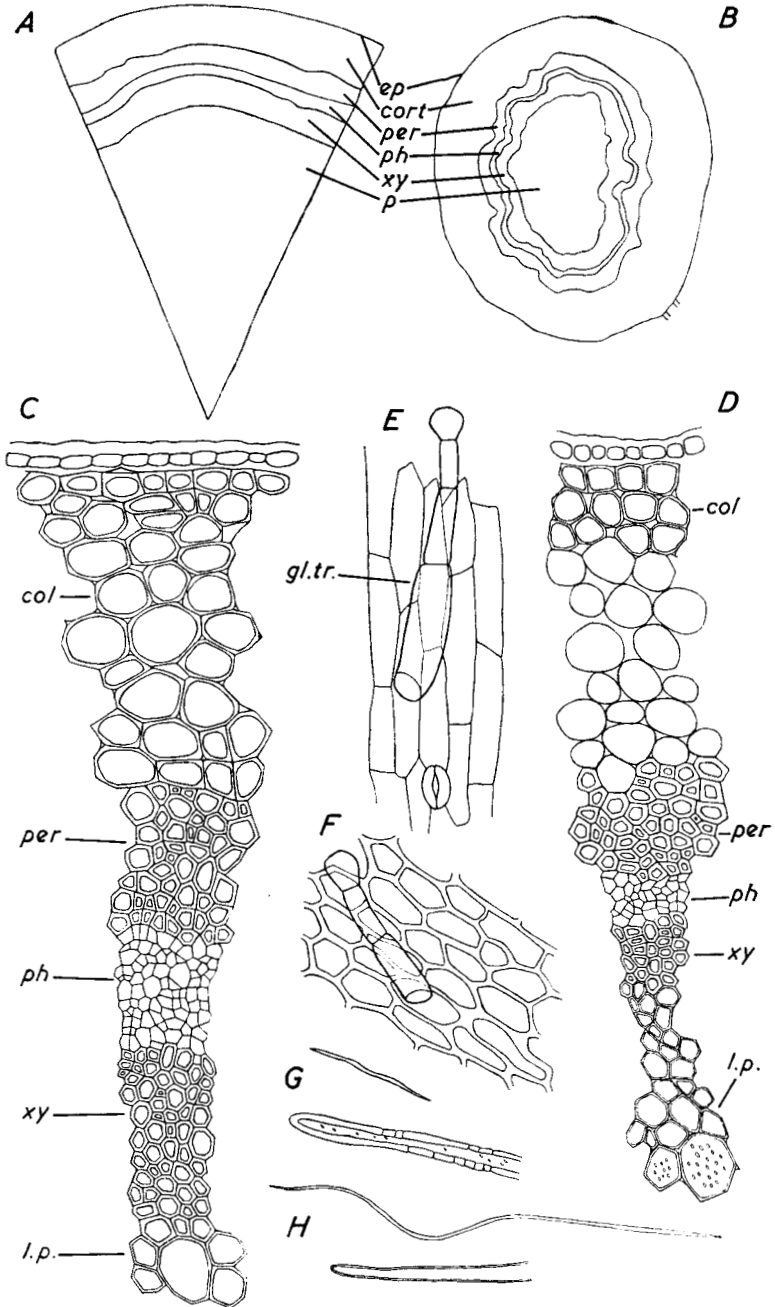


FIG. 7. *Digitalis lanata* L. Pedicel and inflorescence axis. A, Tissue plan of transverse section of inflorescence axis. B, Tissue plan of transverse section of pedicel, both $\times 17$. C, Transverse section of inflorescence axis. D, Transverse section of pedicel. E, Epidermal cells of inflorescence axis. F, Epidermal cells of pedicel, all $\times 170$. G, Fibre from pedicel $\times 50$, part of same $\times 170$. H, Fibre from inflorescence axis $\times 50$, part of same $\times 170$. col, collenchyma; cort, cortex; ep, epidermis; gl. tr., glandular trichome; l.p., lignified pith; per, pericycle; ph, phloem; p, pith; xy, xylem.

xylem is entirely lignified, the polygonal vessels with straight and thickened walls are 8–20 μ in diameter, the thickening is annular and spiral. The central pith cells are polygonal, lignified and pitted (Fig. 7, D).

Inflorescence axis. The histology of the inflorescence axis is similar to that of the pedicel, the differences only will be noted. The epidermal cells are thin walled and larger, L, 80–120–160 μ , T, 14–22–35 μ , (Fig. 7, E). The trichomes are not so numerous, 5–9–11 per sq. mm. The cortex is mainly of collenchyma, although this factor varies with the age of the axis. The fibres, 8–30 μ in diameter, have thinner walls without pits and are longer—up to 2.5 mm. (Fig. 7, H). The ring of vascular tissue is nearer to the periphery of the organ in the axis than in the pedicel (Fig. 7, A and C).

DISCUSSION

The diagnostic characters, other than the abundance of glandular trichomes, which are the most valuable in identifying the inflorescence, when in admixture with the leaf⁹, are as follows.

Corolla. Epidermal cells not beaded. Corolla pigments appearing pink in chloral hydrate solution.

Androecium. Elongated epidermal cells from the filament. Epidermal cells not beaded: fibrous layer from anther wall: pollen grains.

Gynaecium. Elongated epidermal cells from style: epidermal cells not beaded: ovules.

Fruit. Sclerenchymatous cells from fruit wall: reticulate parenchyma from placenta: epidermal cells not beaded.

Seed. Lignified reticulate cells from the testa: storage tissue containing oil and protein.

Pedicel. Elongated, thickened epidermal cells: sclerenchymatous fibres: lignified, pitted pith cells.

Inflorescence axis. Elongated epidermal cells, not beaded: sclerenchymatous fibres: lignified pith cells.

This inflorescence differs from that of *D. purpurea* L.¹ in the following characters.

Calyx. Beaded epidermal cells: mainly smooth cuticle: greater Stomatal Index: Non-glandular trichomes fewer and longer: Glandular trichomes more numerous and longer: Absence of sclerenchymatous fibres and starch sheath.

Corolla. Stomatal index greater: Non-glandular trichomes fewer and shorter.

Androecium. Glandular trichomes present on filament and anther lobes.

Gynaecium. Stomatal index less: fewer trichomes: glandular trichomes present on style.

Fruit. Striated cuticle: fewer trichomes: sclerenchymatous cells neither pitted nor U-shaped.

Pedicel. Thickened epidermal cells: smooth cuticle: glandular trichomes fewer and longer: non-glandular trichomes absent: pith cells pitted and lignified.

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Inflorescence axis. Trichomes as on the pedicel: pith cells not pitted. When the inflorescences of *D. lanata* and *D. purpurea* occur together in a powder the former may be identified by means of the following characters: beaded epidermal cells: pubescent androecium and style: regularly thickened, non-pitted sclerenchymatous cells of the fruit wall.

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After Mr. Cowley presented the paper there was a DISCUSSION.