

DATURA LEICHHARDTII MUELL. EX BENTH. STRUCTURE OF THE FLOWER

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Received March 18, 1963

The structure of the flower of *Datura leichhardtii* is described and compared with the other species of *Datura* so far investigated.

THE characters of the leaf and stem and the nature of the alkaloidal constituents of *Datura leichhardtii* Muell. ex Benth. have already been described (Evans and Stevenson, 1962a; Evans and Stevenson, 1962b). As a prerequisite to a breeding programme involving this and other species of *Datura* it is desirable to have available descriptions of the flowers to facilitate comparison of the hybrid and parent plants. The only two species of *Datura*, the flowers of which appear to have been studied in detail, are *D. stramonium* (Wallis and Rohatgi, 1952a) and *D. innoxia* (Santos, 1927; Wallis and Rohatgi, 1952b). A study of *D. leichhardtii* flowers was therefore undertaken. The source of the plant material was cited previously (Evans and Stevenson, 1962a) and differences between samples of different origin are noted in the text below; otherwise the descriptions given apply generally to all the samples examined.

D. leichhardtii and *D. pruinosa* differ from all other species of *Datura* in the small size of their flowers. With *D. leichhardtii* the corolla is up to about 3.5 cm. in length and the calyx one-half to three-quarters this length. After fertilisation the flower becomes pendent, the calyx shrivels above and becomes accrescent below the line of abscission, and a globose spiny fruit develops.

ANATOMICAL STRUCTURE

Calyx

At the bud stage the calyx is conical and slightly ribbed, becoming inflated and cylindrical before the corolla emerges. It splits into five small, often unequal, teeth and its form, above the line of abscission, when slit longitudinally and flattened is indicated in Fig. 1, A. Each sepal has a well-marked midrib passing from the base of the calyx to the tip of the lobe. The midrib is flanked on either side by another vein which joins it near the base of the lobe. Between these veins, smaller ones anastomose throughout the length of the tube. A transverse section of the calyx, some aspects of the outer and inner epidermis and trichomes, are shown in Fig. 1.

The outer epidermal cells are covered externally with a smooth cuticle and in general, in surface view, they appear polygonal with either straight or slightly sinuous anticlinal walls; their form varies according to the position on the calyx. Cells of the lobe, L and T = 9 to 21 to 27 to 33 μ and R = 12 to 18 to 24 to 30 μ (Fig. 1,C), are somewhat smaller than those lower down the tube, L and T = 15 to 27 to 35 to 61 μ and R = 12 to 30 μ .

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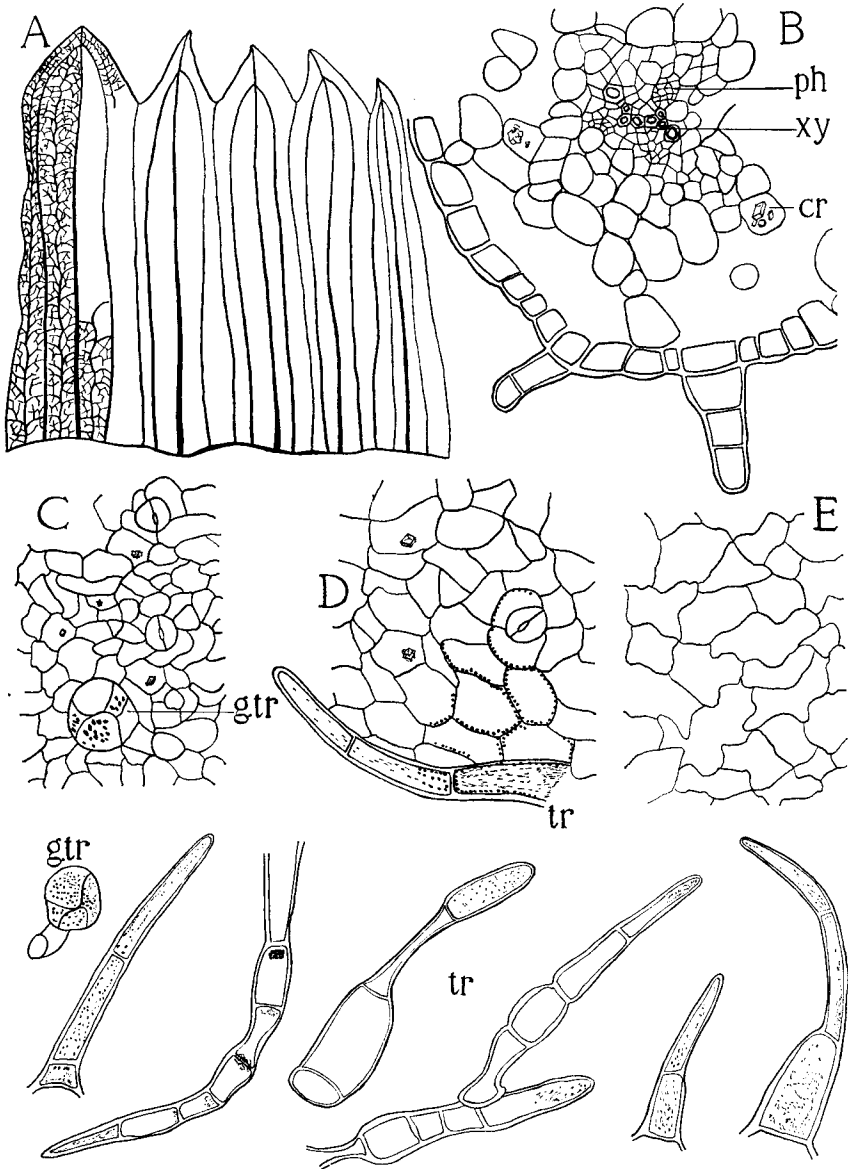


FIG. 1. *Datura leichhardtii* Muell. ex Benth. Calyx. A, calyx above the line of abscission, slit longitudinally and spread out, showing venation, $\times 2$. B, transverse section through the midrib at the middle of the lobe. C, outer epidermis of lobe. D, ditto at line of abscission. E, inner epidermis above the line of abscission. cr, crystals of calcium oxalate; g.tr, glandular trichome; ph, phloem; tr, covering trichomes; xy, xylem. All $\times 240$.

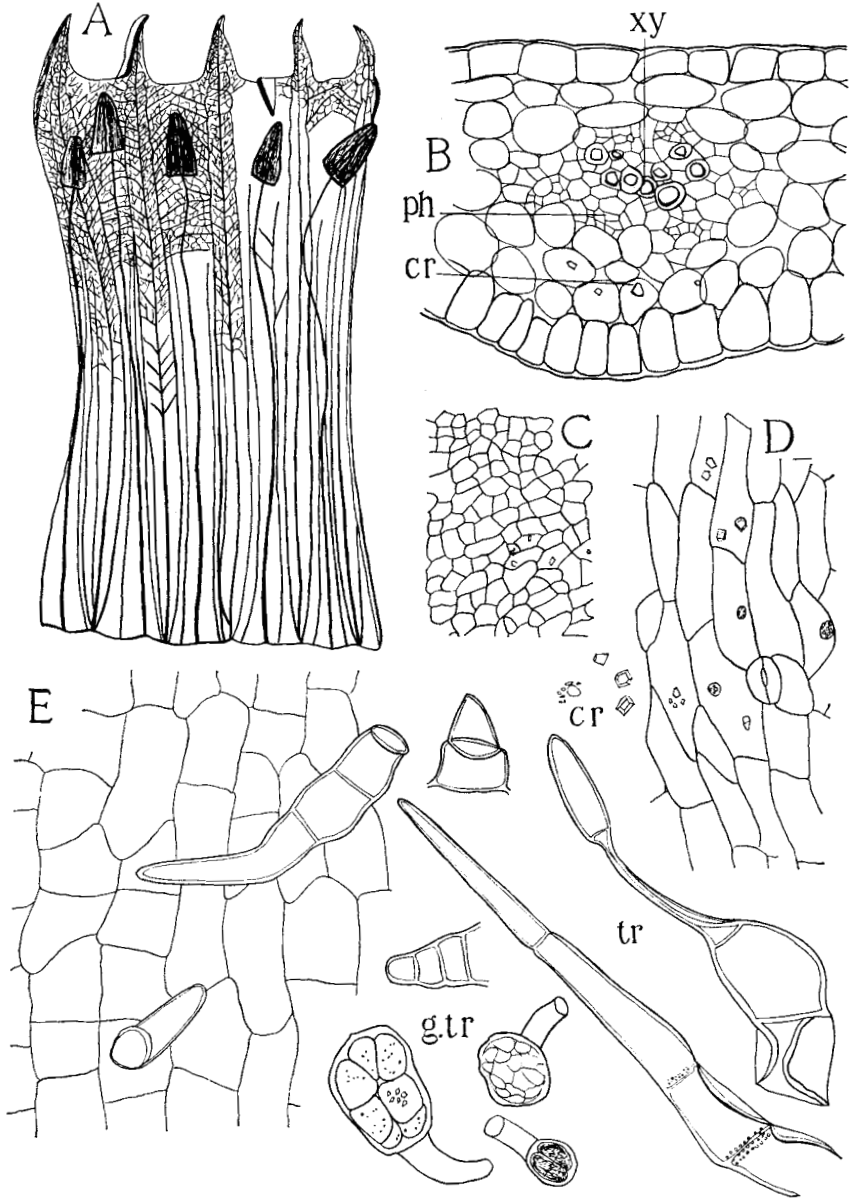


FIG. 2. *Datura leichhardtii* Muell. ex Benth. Corolla. A, slit longitudinally and spread out to show the form, venation and stamens, $\times 5$. B, transverse section through midrib of corolla at base of tube. C, D, E, outer epidermis of lobes, middle and lower part of tube respectively. cr, crystals of calcium oxalate; g.tr, clavate glandular trichomes; ph, phloem; tr, covering trichomes; xy, xylem. All $\times 240$.

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Those epidermal cells overlying the main veins are longitudinally elongated, $L = 18$ to 63μ and $T = 15$ to 42μ . Cells along the line of abscission possess a granular lining to the walls, $L = 30$ to 70μ and $T = 15$ to 60μ (Fig. 1, D), and those below the line of abscission measure $L = 18$ to 69μ and $T = 12$ to 39μ . Stomata of the anisocytic or anomocytic type are of frequent occurrence over the whole of the calyx, except over the veins where they are sparse. Isolated crystals of calcium oxalate occur as prisms, rosettes and rounded masses throughout the epidermal layer. Both glandular and covering trichomes occur over the outer surface of the calyx and are most numerous along the margins of the lobes, especially on samples raised in the greenhouse. The glandular clavate trichomes possess a multicellular head of usually 4 to 8 cells, diameter 33 to 60μ and a single celled stalk of length 18 to 27μ (Fig. 1, g.tr). Uniseriate covering trichomes, 75 to 210μ in length and consisting of 1 to 2 to 3 to 8 cells possess somewhat warty walls and often an enlarged basal cell of diameter 12 to 48μ . Frequently, one cell may be flattened at right angles to the planes of adjacent cells. A few branched trichomes were observed on greenhouse plants (Fig. 1, g.tr).

The inner epidermis of the lobes of the calyx resembles the outer epidermis. At a point above the line of abscission the epidermal cells of greenhouse samples have a somewhat sinuous outline in surface view, L and $T = 15$ to 82μ (Fig. 1, E.); they may possess a few glandular and covering trichomes, the latter generally of three cells, narrower than those trichomes of the outer epidermis and with no swollen basal cell. The inner epidermis of the calyx of Australian-grown flowers, taken at the same level, differed in having less sinuous anticlinal walls, more stomata and more trichomes of both types. At the line of abscission the inner epidermal cells resemble those of the outer epidermis and contain the characteristic granular deposit along the walls. Just below the line of abscission the cells are polygonal, or slightly sinuous, in outline and may contain irregular masses of calcium oxalate. At this level there were clothing and glandular trichomes but these were not observed on the inner epidermis towards the base of the calyx.

The structure of the calyx in transverse section and the form of the calcium oxalate crystals in the mesophyll are similar to those of *D. stramonium* (Wallis and Rohatgi, 1952a) (Fig. 1, B).

Corolla

In general the yellowish-white corollas of flowers formed in the greenhouse in Nottingham remained unopened each as a ribbed tube with five incurved pointed lobes. Avery and Satina (1959) illustrate *D. leichhardtii* with similar corollas, but several of the Kew herbarium specimens of Australian plants and dried material obtained from Australia have open corollas. The form of the corolla and its attached stamens when slit longitudinally and spread out is shown in Fig. 2, A.

Surface features of the outer and inner epidermal cells at different levels of the corolla are shown in Fig. 2, C to E. They have straight, or slightly sinuous anticlinal walls, their form and size varying according to

their location. On the lobes they are relatively small, L and T = 6 to 9 to 18 to 24 μ , R = 6 to 9 to 15 to 18 μ and often contain appreciable amounts of calcium oxalate as prisms or cluster crystals. Stomata are infrequent. Covering trichomes, length 45 to 130 μ , along the margins of the lobes are similar to, but not as large as, those of the calyx and generally consist of two cells; a few have the basal cell enlarged, diameter 6 to 24 μ . A few glandular trichomes, similar to those of the calyx, were observed (Fig. 2, g.tr). On the upper part of the tube the outer epidermal cells are somewhat more elongated; Australian samples contained prismatic crystals and British samples a mixture of prisms, clusters and masses of calcium oxalate. At the middle of the tube the outer epidermal cells are much larger, distinctly elongated and rectangular to polygonal in form. L = 36 to 60 to 90 to 111 μ , T = 9 to 12 to 18 to 27 μ and R = 15 to 18 to 21 to 24 μ (Fig. 2, D). Stomata are of the anisocytic type and there are small clothing trichomes of 1 to 4 cells, length 15 to 150 μ (Fig. 2, tr). There are a few glandular trichomes and numerous calcium oxalate crystals as single prisms and clusters. Towards the base of the corolla the outer epidermal cells bear clothing trichomes composed of relatively short cells, often somewhat collapsed or folded, total length 15 to 315 μ (Fig. 2, tr). The epidermal cells at the base of the corolla are indicated in Fig. 2, E. They contained isolated crystals of calcium oxalate and possessed a few trichomes. No stomata were observed.

Except for their generally smaller size, the cells of the inner epidermis resemble those of the outer epidermis and stomata become infrequent or absent towards the base of the corolla. A few clavate glandular trichomes occur on the lobes and covering trichomes in most regions, often up to 315 μ in length with a basal cell diameter of 15 to 60 μ . Some cells are often characteristically flattened (Fig. 2, tr).

Transverse sections through the lobes of the corolla show a mesophyll of about 5 layers of isodiametric, closely compacted, thin-walled cells, R = 9 to 12 to 18 to 27 μ and T = 9 to 15 to 21 to 30 μ . Prismatic crystals of calcium oxalate occur irregularly throughout the mesophyll together with small granules which stain blue with iodine solution. Some sections showed an almost complete crystal layer in both the upper and lower epidermal cells; in other sections this was not so obvious. Transverse sections through other parts of the corolla are similar and at the base of the corolla, through the midrib (Fig. 2, B) show a vascular strand composed of groups of phloem and spirally thickened vessels surrounded by mesophyll cells with intercellular air spaces between them.

Stamens

The five epipetalous stamens, alternating with the corolla lobes, are about 2 cm. in length and have white anthers, 3.5 mm. in length, which dehisce longitudinally before the corolla reaches its maximum size.

The epidermal cells of the free part of the filament are subrectangular to polygonal in outline and elongated in the direction of the long axis, L = 45 to 189 μ and T = 9 to 21 μ . Neither stomata nor trichomes occur in this region. That part of the filament adnated to the corolla has epidermal

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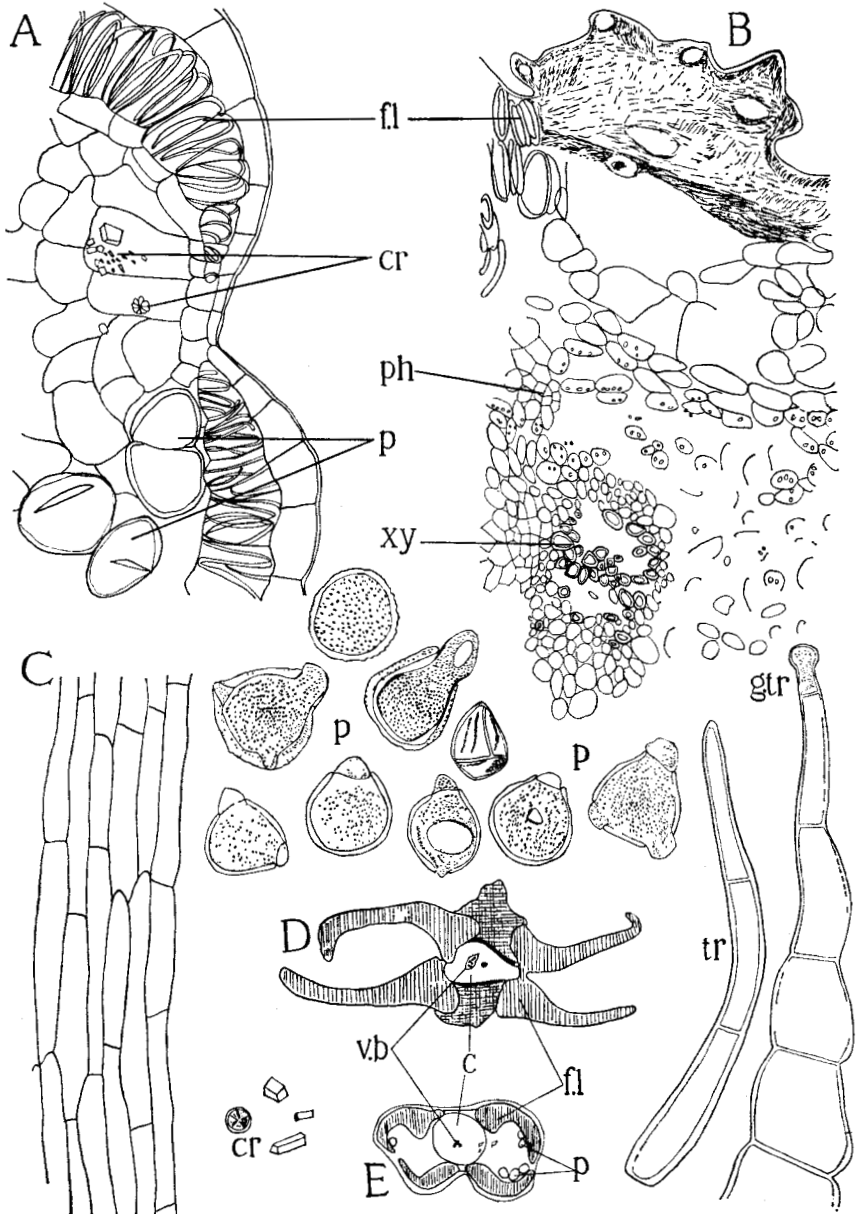


FIG. 3. *Datura leichhardtii* Muell. ex. Benth. Stamen. A, transverse section through anther wall at the line of dehiscence; B, transverse section through the connective; C, epidermis of the filament, surface view. All $\times 240$. D, diagram of transverse section through anther; E, ditto of very young flower. Both $\times 25$. c, connective; cr, crystals of calcium oxalate; fl, fibrous layer; g.tr, glandular trichome; p, pollen grains; ph, phloem; tr, clothing trichome; v.b, vascular bundles; xy, xylem.

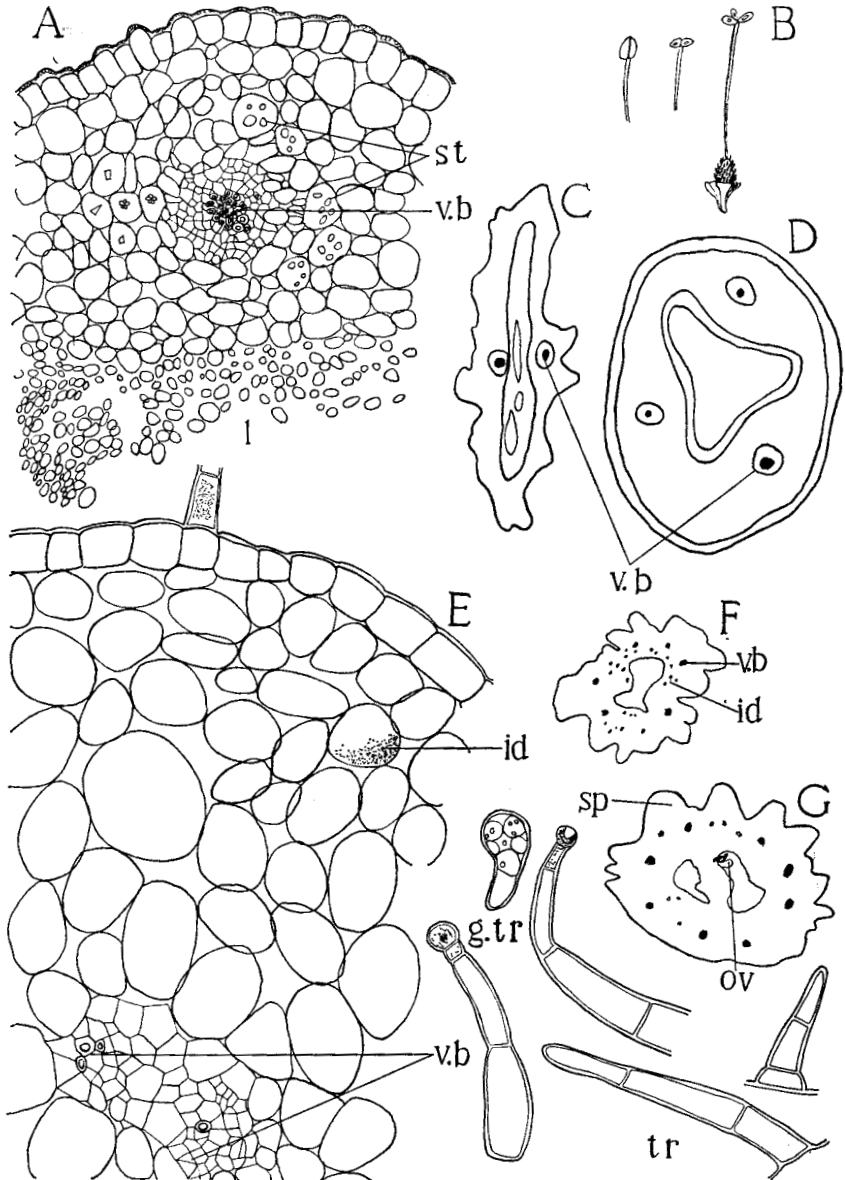


FIG. 4. *Datura leichhardtii* Muell. ex Benth. A, transverse section through the style, $\times 240$; B, gynaecium and forms of the stigma $\times 1$; C, D, transverse sections through the style, $\times 60$; E, transverse section through spine on ovary wall, $\times 240$. F, transverse section through ovary just below insertion of style. G, ditto middle portion, both $\times 7$. *g.tr*, glandular trichomes $\times 240$; *id*, idioblast; *l*, lacuna; *ov*, ovules; *sp*, spine; *st*, starch granules; *tr*, covering trichomes of the outer epidermis $\times 240$; *v.b*, vascular bundles.

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cells shorter and broader than those of the free part and resembling those cells of the corresponding level of the corolla. Covering trichomes are frequent, generally conical or filamentous in form, often up to 480μ in length and composed of 2 to 3 to 4 to 6 cells (Fig. 3, tr). Some terminate in a relatively small single-celled gland (Fig. 3, g.tr). Other unicellular trichomes are similar to those on the corolla. A transverse section through the free portion of the filament is similar to that of *D. stramonium* (Wallis and Rohatgi, 1952a).

The outer portion of the connective is composed of spongy parenchyma, having large numbers of lacunae, and this loosely links the lobes to the central area. Several layers of parenchyma, the outer ones coloured yellow or brown, and containing many small rounded bodies of unknown composition, surround the vascular cylinder. The latter consists of small groups of phloem around a group of small, spirally thickened vessels which are somewhat elliptical in transverse section. A lacuna is generally evident (Fig. 3, B, D). In the young anther, spongy parenchyma and air spaces are absent from the connective (Fig. 3, E). The outer epidermis of the anther lobes is composed of cells elongated in the longitudinal direction, has a well-marked cuticle and possesses many filamentous trichomes of 2 to 5 cells and up to 390μ in length. For the epidermal cells, $R = 12$ to 18 to 30 to 39μ and $T = 24$ to 42 to 60 to 90μ . In the proximity of the line of dehiscence, the fibrous layer of the anther wall is one cell thick, but becomes 2 to 4 cells thick in the region where it joins the connective; in surface view it resembles that of *D. stramonium* and it gives a slight reaction for lignin when tested with phloroglucinol solution followed by concentrated hydrochloric acid (Fig. 3, A, B, D, E). The pollen grains (Fig. 3, p), mounted in cold lactophenol, are generally spherical in outline having three, usually well-marked, germinal pores 6 to 12 to 18 to 27μ in diameter and faint germinal furrows. The surface of the exine is irregularly granular. Pollen grain diameter varied somewhat with the many samples examined; 1,500 grains were measured and the diameters, excluding projecting pores, were 24 to 45 to 54 to 69μ . 8 per cent of the grains measured exceeded 54μ and 0.7 per cent exceeded 60μ .

Gynaecium

The conical ovary is about 3 mm. wide at the base, 4 mm. long and is covered by four areas of spines. The style when fully developed is about 3 cm. in length and thickens towards the stigma; the latter is usually capitate but may form two or three divergent lobes (Fig. 4, B).

Transverse sections indicate a single lacuna directly under the insertion of the style but the ovary is two-celled below this level (Fig. 4, F, G). The ovary wall bears spines and trichomes. In surface view the epidermal cells of the ovary wall are irregular in shape, $L = 9$ to 45μ , $T = 9$ to 33μ and $R = 21$ to 30μ . The structure and contents of the mesophyll and septum resemble those of *D. stramonium*.

The epidermal cells of the spines are elongated in the direction of the axis, $L = 22$ to 120μ , $T = 9$ to 54μ and $R = 15$ to 24μ , and contain variously shaped crystals of calcium oxalate. In transverse section the

spines show a ring of small vascular bundles surrounded by almost isodiametric parenchymatous cells many of which contain crystal sand (Fig. 4, E). The spines of mature fruits also show in their basal portions a ring of about 12 to 13 groups of lignified elements, each group consisting of a few spirally thickened vessels surrounded by lignified parenchyma. Towards the apex of the spine the ring of lignified tissue is complete. Clothing and glandular trichomes are associated with the spines of the ovary, the two- or three-celled clothing forms being most numerous. The glandular trichomes are of two types, the common clavate type with a multicellular head and those with a multicellular uniseriate stalk and a single-celled glandular head (Fig. 4, g.tr).

The epidermal cells of the style are elongated in the direction of the main axis; they may contain rosettes, prisms or irregular masses of calcium oxalate and in transverse section show convex outer surfaces, $L = 39$ to 105μ , $T = 9$ to 21μ and $R = 18$ to 27μ . The cuticle is longitudinally striated, stomata are rare and no trichomes were observed. In transverse sections, two different forms of the style were noted. One (Fig. 4, C) is irregular and flattened in outline with an oval central area of thin-walled cells and irregular lacunae. On either side of the central area is a vascular strand. The other form (Fig. 4, D) is rounded or slightly oval in transverse section with a triangular to three-lobed central area of thin-walled, rounded cells (L and $T = 6$ to 15μ) and in the centre of this area is a large lacuna of the same shape. The outer parenchyma supporting the central zone consists of 2 to 12 rows of almost isodiametric cells (L and $T = 9$ to 36μ) and containing small round starch grains and isolated clusters and prisms of calcium oxalate. Three vascular strands, alternating with the lobes of the central area, are situated in the outer parenchyma (Fig. 4, A). These two styles are correlated with the form of the stigma which may be capitate with a vertical groove on either side, or two- or three-lobed, with the lobes spreading and attached to one another and the top of the style, at their bases (Fig. 4, B). The three-lobed stigma corresponds to the style with three vascular strands. The oval-shaped stigma is covered, except for the vertical grooves, by a papillose receptive surface which arises from a central area of small-celled tissue; pollen grains may be attached. There is a vascular bundle on either side of the central area. In those stigmas with divergent lobes, each lobe corresponds essentially to one half of the oval shaped stigma described above and in transverse section shows a reniform outline.

CONCLUSION

The flowers of *D. leichhardtii* are smaller than those of all but one other species of *Datura*; their histological features closely resemble those of the flowers of *D. stramonium* and *D. innoxia* which are the only other flowers of the genus *Datura* which have been described in detail (Wallis and Rohatgi, 1952a, b). The pollen grains afford some distinguishing characters; they are very similar to those of *D. stramonium* but are slightly smaller in size being about 24 to 45 to 54 to 69 μ in diameter, while those of *D. stramonium* are about 48 to 60 to 78 μ in diameter. The pollen grains

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are, however, markedly different from those of *D. innoxia*, being slightly smaller in size and bearing quite different marking of the exine. The clothing trichomes of the calyx, with flattened cells similar to those observed on the leaves, and the uniseriate trichomes with a single glandular head are characters not common to the flowers of *D. innoxia* and *D. stramonium* respectively.

Acknowledgement. One of us (A.C.A.) is indebted to the "Comissão Coordenadora da Investigação para a OTAN", Lisbon, Portugal, for the award of a scholarship, during the term of which this study was undertaken.

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