STUDIES ON DATURA LEICHHARDTII MUELL. EX BENTH.

PART I. THE ANATOMY OF THE LEAF AND STEM

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Datura leichhardtii is readily distinguished from other species of the genus by its general morphology. Although similar to that of D. stramonium, the microscopy of the leaf differs in the length of the clothing trichomes and often in the form of the calcium oxalate crystals; it may be distinguished from other members of the Section Dutra, with the exception of D. metel, by the form and abundance of trichomes. D. leichhardtii differs from D. metel in possessing on the lamina of the leaf, glandular trichomes with a uniseriate stalk and a single-celled head. The values for palisade ratio and stomatal index are within the same range as those of allied species.

THE genus *Datura* has been extensively investigated from the viewpoint of taxonomic classification, genetics, commercial production of crude drugs and the study of alkaloid biogenesis. Most attention has focused on those species which are utilised commercially either as sources of alkaloids or for galenical manufacture and adequate descriptions are available for these plants. One species which has received little attention, either anatomically or chemically is *D. leichhardtii* Muell. ex Benth., a plant named by Mueller (1855) and subsequently described in Bentham's (1868) *Flora Australiensis*. Its natural distribution appears to be limited to Australia where it has been cited as occurring along the banks of the rivers of Western Australia and in Queensland (Bentham, 1868; Ewart and Davies, 1917; Hurst, 1942; Gardner and Bennetts, 1953).

In addition to the possible usefulness of *D. leichhardtii* as a source of tropane alkaloids, it would also appear to be potentially useful in the study of the genetics of alkaloid production in the genus and, for breeding experiments involving interspecific hybrids. In this connection Blakeslee (Avery, Satina and Rietsema, 1959) has shown that this plant, used as the female parent, is capable of forming viable crosses with seven other herbaceous *Datura* spp. and with two others by embryo dissection. In this way it has been used as a bridging species for otherwise, often incompatible, crosses. This species forms an obvious link between Safford's (1921) Section I, Stramonium Gaertner and Section II, Dutra Bernhardi; it resembles the former in its general habit, leaves and flowers but is included in the latter because of *D. leichhardtii* have been studied by Blakeslee and compared with other species of the genus (Avery, Satina and Rietsema, 1959).

In this paper we record the anatomical characters of the leaves and stems of this plant.



FIG. 1. Datura leichhardtii Muell. ex Benth. A1 to A4, general diagrams, $\times 10^{\circ}$ of transverse sections of stem taken at positions 1 to 4 on A. B, epidermis of stem $\times 180$. C, young plant $\times \frac{1}{4}$. D, mature capsule $\times \frac{1}{4}$. E, flower, Nottingham plant $\times \frac{1}{4}$. b, bud; b.c, base of clothing trichome, b.g, base of glandular trichome; ca, calyx; co, corolla; cor, cortex; ed, endodermis; ep, epidermis; f, self-pollinated flower which has become pendant, with shrivelled perianth; i.f, internal fibres; p.f, pericyclic fibres; ph, phloem; p.x, primary xylem; r.x, medullary ray; sc.x, secondary xylem; s.x, sandy crystals of calcium oxalate.

PLANT MATERIAL

The *D. leichhardtii* for this investigation was obtained in 1952 as dried specimens, including seeds, collected from an unspecified source in Australia. From the seeds, mature plants were raised in Nottingham and the propagation continued over a number of years from seed collected annually. The climate proved generally unsuitable for field-work with this species, but in warm dry summers some reasonably mature plants were produced in the open. Most of our material was grown in a temperate greenhouse. We have also examined the type specimen and others at the Kew Herbarium.

ANATOMICAL STRUCTURE

Plants grown in Nottingham (Fig. 1, C) possessed the macroscopical characters ascribed by Bentham (1868) to D. leichhardtii and were similar to the Kew Herbarium specimens. Except during the hot summer of 1959, we have not succeeded in obtaining flowers with fully expanded corollas. The latter remain folded (Fig. 1, E) and after self-fertilisation the pedicel bends over and the dried remains of the perianth often adhere to the developing fruit. Avery and Satina (1959) also illustrate D. leichhardtii with an unexpanded corolla but several of the Kew herbarium specimens, collected in Australia, have fully opened flowers. This would seem to be a character influenced by environment as is also the development and dehiscence of the fruit. After pollination, the lower portion of the calvx develops into a flange which may be appressed to (Fig. 1, D) (also Avery and Satina, 1959) or reflexed away from (Gardner and Bennetts, 1953) the fruit. In dry conditions the capsule dehisces regularly into four valves which hinge back to reveal the seeds tightly packed in two Sometimes the seeds may be scattered as a result of the rapid loculi. splitting of the fruit wall; during or after dehiscence the whole capsule may fall from the plant. Damp conditions tend to promote less regular dehiscence and the pericarp disintegrates into a number of irregular soft portions which fall with the seeds leaving only the flange and septum attached to the axis.

STEMS

The herbaceous stem has a bicollateral vascular system and Fig. 1, A1-A4 shows the distribution of tissues at different levels of the plant axis; the principal variation occurs in the amount of secondary xylem and presence of pericyclic and internal fibres at the different levels. Except in the instances stated, the following description applies to stems taken at any level.

The epidermis consists of elongated cells showing in surface view occasional striations of the cuticle. Fine pores traverse the unevenly thickened anticlinal walls and calcium oxalate as single prismatic crystals is occasionally evident. Anisocytic stomata are frequent and with older stems, often have associated with them brown amorphous material. Longitudinal cracks which sometimes occur in the epidermal layer just

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FIG. 2. Stem of *Datura leichhardtii* Muell. ex Benth. A-E transverse sections. A, cortical region; B pericycle and phloem; C, secondary wood; D, primary xylem; E, internal phloem; F, tangential longitudinal section of secondary xylem. All \times 180. *a*, starch; *c*, cambium; *col*, collenchyma; *cu*, cuticle; *cx*, calcium oxalate crystal; *ed*, endodermis; *ep*, epidermis; *i.f*, internal fibres; *i.ph*, internal phloem; *par*, parenchyma; *p.f*, pericyclic fibre; *ph*, phloem; *p.x*, primary xylem; *r.c*, medullary ray cell in the phloem; *r.x*, medullary ray in the xylem; *s.x*, sandy crystals of calcium oxalate; *v*, vessel; *x.f*, xylem fibre; *x.p*, xylem parenchyma.

above soil level are filled with a brown disorganised callus tissue. For the epidermal cells, R = 18 to 20 to 30 to 45 μ ; T = 24 to 30 to 50 to 60 μ and L = 36 to 60 to 120 to 144 μ (Fig. 1, B; 2, A). The epidermis of older stems bears only the remains of trichome bases (Fig. 1, B), but both clothing and glandular trichomes are present on the young stems. In structure, the trichomes resemble those of the leaves, described below, with the slight exception that those glandular trichomes with a single-celled head and a uniseriate stalk do not usually show warty walls (Fig. 6, A).

The hypodermal collenchyma in the young stems shows thickening in the corners of the cells, whereas in older stems the thickening extends around all the walls. Individual cells are longitudinally and usually tangentially elongated. R = 36 to 84μ ; T = 36 to 168μ and L = 120to 360μ (Fig. 2, A). This layer merges into underlying thin-walled parenchyma of relatively large cells which are oval, round or angularly flattened in transverse section R = 75 to 300μ ; T = 120 to 360μ and L = 75 to 150μ . Intercellular spaces are present and single starch grains up to 15μ in diameter are contained in the cells. The endodermis is clearly indicated as a starch containing sheath, individual starch grains resembling those of the cortex. In transverse section the cortex consists of about eight layers of cells (Fig. 2, A, B).

A discontinuous ring of small groups of, or isolated, fibres, oval or rounded in transverse section with highly refractive walls and staining a pale pink with phloroglucinol solution followed by concentrated hydrochloric acid, indicates the pericycle (Fig. 2, B). These fibres can be isolated from an alkali maceration and show tapered or rounded ends, a length of about 1.8 to at least 3.5 cm., a lumen diameter of 24 to 60μ , wall thickness of 3 to 8μ and sometimes marked swellings along their length (Fig. 3, p.f.).

The phloem (Fig. 2, B) consists of sieve tissue traversed by secondary medullary rays, 1 to 3 cells wide with individual cells measuring R = 15 to 21 to 33 to 45 μ and T = 12 to 15 to 30 to 40 μ . The larger sieve tubes are up to about 30 μ in diameter. Idioblasts, R and T = 10 to 96 μ and L up to about 132 μ , containing sandy crystals of calcium oxalate occur scattered throughout the phloem; phloem fibres are absent.

Interior to the cambium the completely lignified secondary xylem forms a cylinder consisting of vessels, fibres, secondary medullary rays and xylem parenchyma (Fig. 2, C). Vessels are scattered evenly throughout the wood either singly, in pairs or in small groups; they are often radially elongated, T = 15 to 25 to 65 to 96 μ and R = 24 to 36 to 100 to 132 μ . Vessel members, excluding the protuberances are 80 to 120 to 300 to 360 μ long and may be isolated for examination, together with other components of the wood by use of Schulze's macerating fluid. The vessel pitting varies from simple slits to alternately arranged bordered pits. Occasional tyloses are evident in the vessels of older parts of the stem.

The wood fibres, length 200 to 350 to 700 to 720 μ , diameter 9 to 15 to 27 to 36 μ and wall thickness 2 to 5 μ have pits ranging from simple slits to others with extended pit apertures. Wood fibres adjacent to a



FIG. 3. Datura leichhardtii Muell. ex Benth. Isolated lignified elements of stem \times 180. *i.f.*, internal fibres; *p.f.*, pericyclic fibres; *p.x.*, primary xylem; *r.c.*, medullary ray cells; *v.e.*, vessel elements; *v.r.*, vessel element with medullary ray cells attached; *x.f.*, xylem fibre; *x.p.*, xylem parenchyma.

ray may possess a scalloped outline and a few have bifurcated ends (Fig. 3, x.f.).

In young stems the medullary rays are mainly uniseriate in transverse section and, up to about 60 cells deep (Fig. 2, C; 4, A); similar sections of older stems, particularly from material grown in Australia and raised in the field in England, show rays 1 to 2 to 3 to 4 cells wide and 3 to 5 to 10 to 13 cells deep (Fig. 4, B). For individual cells, R = 6 to 15 to 30 to 42 μ , T = 3 to 6 to 24 to 36 μ and L = 15 to 20 to 60 to 81 μ but for some material that was grown under glass, the uniseriate rays were difficult to distinguish from wood parenchyma cells because of their often increased length, L = 24 to 30 to 180 to 195 μ (Fig. 2, F). The cells of the medullary rays contain small starch granules (2 μ) and the walls may have simple or bordered pits according to the nature of the adjacent cell; xylem parenchyma is scanty, apotracheal and diffuse and contains abundant starch granules about 2 μ in diameter; the cells measure R and T = 9 to 12 to 16 μ , L = 28 to 90 to 196 to 250 μ (Fig. 2, C; Fig. 3, x.p.).



FIG. 4. Datura leichhardtii Muell. ex Benth. Tangential longitudinal sections of the secondary xylem. A, Nottingham greenhouse plant. B, Australian plant. Both \times 45. r.x, medullary rays; x.f, xylem fibres; x.p, xylem parenchyma; v, vessel.

Groups of primary xylem contain radially arranged vessels with spiral or scalariform thickenings (Fig. 2, D; 3, p.x.). Approximately four cells interior to the primary xylem is a ring of compact groups of small thin-walled cells constituting the internal phloem (Fig. 2, E). Adjacent to the inner phloem are single, or small groups of, fibres having highly refractive cell walls which stain a pale pink with phloroglucinol and hydrochloric acid. They may be isolated from a 5 per cent potassium hydroxide maceration (Fig. 2, E; 3, i.f.); length 1.6 to at least 8.5 mm., lumen diameter 18 to 33 μ , thickness of walls 3 to 6 μ .

The medulla is composed of a relatively large-celled parenchyma, some cells of which contain starch granules similar to those of the cortex and others, sandy crystals of calcium oxalate. In longitudinal sections the cells often appear to be arranged in vertical columns. R and T = 165 to 200 to 270 μ and L approximately 120 μ .

LEAVES

Lamina, Interneural Region

The lamina consists of an upper and lower epidermis with stomata and trichomes, a single layer of palisade cells, collecting cells containing calcium oxalate crystals and about 3 to 4 layers of spongy mesophyll (Fig. 5, B). It measures about 175 to 275μ in thickness.

The upper epidermis consists of cuticularised cells with almost straight anticlinal walls, length 18 to 30 to 70 to 105 μ , breadth 12 to 20 to 50 to 60 μ and depth 15 to 18 to 24 to 30 μ . Stomata are mainly of the anisocytic type, elliptical in outline, length 27 to 36 μ and width 8 to 12 μ (Fig. 5, E). The stomatal index is 10.4 to 15 to 19 (English samples) and 19.5 to 21.3 to 24 (Australian samples). The lower epidermis has a smooth, thin cuticle and the anticlinal walls of individual cells are wavy, in outline, length 18 to 30 to 80 to 105 μ , breadth 9 to 20 to 40 to 60 μ , depth 9 to 15 to 21 μ . The stomata resemble those of the upper epidermis. The stomatal index is 15 to 19 to 24 (English samples) and 22.7 to 23.5 to 24 (Australian samples), and the stomatal number ratio is 1.3 to 1.8 to 2.4.

Uniseriate clothing trichomes (Fig. 6, A) occur on both surfaces of the lamina, but particularly along the lower surface of the veins. Thev consist of 1 to 2 to 3 to 4 cells with warty walls, sometimes collapsed at right angles to one another even when examined from fresh material. Length of trichomes 69 to 125 to 200 to 300 μ and with the basal cell, length 35 to 63 to 98 μ , diameter 16.5 to 20 to 30 to 42 μ often funnelshaped at the point of attachment to the epidermis and extending to a diameter of 20 to 40 to 50 to 75 μ . Yellow contents of the trichomes, especially of fresh material, stain with Tincture of Alkanna and contract to a small mass when treated overnight with ethanol and are virtually unaffected by ether. In choral hydrate preparations the trichomes are completely cleared and an occasional small crystal is evident. Small glandular trichomes possessing a unicellular stalk and usually about five cells in the head (Fig. 6, A) are found on both surfaces of the lamina, especially along the veins; their vellow contents respond to chemical reagents in a similar way as those of the clothing trichomes. For the unicellular stalk, length = 9 to 15 to 24 to 27 μ and breadth = 12 to 15 to 21 μ ; for the head, length = 30 to 35 to 50 to 56 μ and breadth = 30 to 35 to 50 to 56 μ . Glandular trichomes, length 132 to 200 to 400 to 432 μ having single celled heads, diameter 12 to 15 to 25 to 32 μ and uniseriate multicellular stalks are occasionally present, especially near the leaf-margin and on the lower surface of the veins. The stalks, usually of three cells, are as warty as the covering trichomes but the glandular head is transparent. Similar trichomes were also found on seedlings of D. stramonium var. tatula.

Counts of trichomes (combined clothing and long glandular) were made for interneural regions of the lower epidermis together with similar counts for other species of *Datura*. For *D. leichhardtii*, *D. stramonium*, *D. ferox* and *D. metel* figures in the range 0 to $4/\text{mm.}^2$ were obtained whereas *D. innoxia* and *D. meteloides* gave figures of about $45/\text{mm.}^2$ and *D.*



FIG. 5. Leaf of *Datura leichhardtii* Muell. ex Benth. A1 to A4, general diagrams, \times 45, of transverse sections taken at positions 1 to 4 on A. B, transverse section of lamina. C, lamina, lower epidermis. D, calcium oxalate crystals from collecting layer of leaf. E, lamina, upper epidermis. B to E \times 180. *cu*, cuticle; *c.x*, calcium oxalate crystal; *l.ep*, lower epidermis; *m*, spongy mesophyll; *p*, palisade layer; *ph*, phloem; *s*, stomata; *u.ep*, upper epidermis; *v.b*, vascular bundle; *x*, xylem.

discolor 11 and 40/mm.² according to the sample. Verzár-Petri and Sárkány (1961) for the lower epidermis quote figures of $17/\text{mm.}^2$ for the long glandular trichomes of *D. innoxia* and $1/\text{mm.}^2$ for the clothing trichomes of various varieties of *D. metel.*

The palisade layer consists of a single layer of cells, height 60 to 70 to 135 to 144μ and palisade ratio 2.3 to 4.8 to 7.5. A crystal layer of calcium oxalate occurs in the collecting cells, many of which contain independent crystal clusters, diameter 9 to 30 to 50 to 60 μ , prisms 9 to 12 to 25 to 42 μ long and 4 to 6 to 18 to 21 μ wide, conglomerates of clusters and prisms and crystal sand (Fig. 5, D). Large cluster crystals were predominant in the Australian sample, individual prisms with associated rosettes in greenhouse plants and, a mixture of crystal clusters and prisms in the English field plants. A small fragment of the leaf of the type specimen showed a mixture of small cluster crystals and prisms.

Midrib

The general structure of the midrib taken at various positions along the leaf is shown in Fig. 5, A1 to A3 and a more detailed illustration of a transverse section through the lower part of the midrib is given in Fig. 7, A. The upper epidermis consists of a layer of straight-walled cells elongated in the direction of the long axis of the leaf and bearing clavate and clothing trichomes similar to those on the lamina. The lower epidermis is similar. Towards the base of the leaf, the hypodermal regions of both upper and lower surfaces are collenchymatous. For individual cells, R and T = 13 to 15 to 27 to 36μ and L = 75 to 120 to 255 to 300μ . The remainder of the cortex consists of parenchymatous cells, R and T = 28 to 33 to 60 to 75 μ and L = 84 to 120 to 250 to 360μ ; some cells contain small starch grains and others, especially towards the petiole, sandy crystals of calcium oxalate.

In transverse section the meristele is arcuate and composed of xylem bounded above and below by phloem. The latter consists of groups of thin walled tissue separated by medullary rays and the wood vessels, with annular, spiral and scalariform thickenings are radially arranged and measure chiefly about 20 to 30 μ in diameter. Unlignified medullary rays, one or two cells wide, pass through the xylem.

Petiole

The distribution of tissues in the petiole is indicated in Fig. 5, A4 and Fig. 7, B. In surface view the epidermal cells of both the adaxial and abaxial surfaces are similar, being elongated with respect to the long axis and having unevenly thickened anticlinal walls, R and T = 24 to 30 to 40 to 48 μ and L = 24 to 40 to 120 to 180 μ . The cuticle of the epidermis is occasionally striated. Stomata, similar to those found on the lamina, are present on the upper epidermis but rarely on the lower and trichomes of the usual types are numerous, particularly along the groove on the adaxial surface. The hypodermal collenchyma 4 to 5 cells deep is continuous beneath the epidermis; its cells contain small starch granules about 2 μ in



FIG. 6. Datura leichhardtii Muell. ex Benth. A, trichomes of stems and leaves. B. petiole, upper epidermis. C, petiole, lower epidermis. All \times 180. a, b, d, e, f, h, l, clothing trichomes; c, i, k, glandular trichomes with unicellular stalk. g, glandular trichome of stem with multicellular stalk; j, ditto of petiole. *b.c*, scar of attachment of clothing trichome; *b.g*, ditto small glandular trichome; *c.x*, calcium oxalate crystal.

diameter. Both the collenchymatous cells and the underlying parenchyma are longitudinally elongated. Two small ridge bundles are embedded in the parenchyma of the ridges on the adaxial surface. Scattered idioblasts containing sandy crystals of calcium oxalate occur throughout the cortical parenchyma, other cells contain single starch grains of diameter 1 to 5 to 7 μ , compound granules each composed of 2 to 3 to 6 components and complex masses of starch granules up to 30 μ in diameter. The meristele resembles that of the midrib; annual and spiral vessels constitute the protoxylem with scalariform thickened vessels of the metaxylem located towards the abaxial perimeter of the xylem.

DISCUSSION

A complete key for the classification of the herbaceous Datura species, based on microscopical characters, cannot be attempted at present owing to the paucity or lack of information on some species. Morphologically the species can be divided into those with pubescent leaves and those having few trichomes on the leaf surfaces and appearing almost glabrous. A1though the actual number of trichomes per mm.² of leaf surface probably varies considerably for any one species, our limited investigations suggest that it can be used to differentiate between the two groups by microscopical means. In this way D. leichhardtii can be distinguished from other members of the Section Dutra, with the exception of D. metel and its The warty-walled clothing trichomes of D. leichhardtii, often varieties. with their characteristic flattened cells, are generally shorter than those of D. stramonium (Timmermann, 1927a), D. innoxia (Timmermann, 1927a; Košová and Chládek, 1957) but resemble those of D. meteloides and D. discolor (Kalemkiarian and Miller, 1957); they may be shorter than (Timmermann, 1927a; Santos, 1927; Košová and Chládek, 1957) or about the same length as (Verzár-Petri and Sárkány, 1961) those of D. metel. Glandular trichomes with a single celled head and a uniseriate stalk, which are of limited occurrence on the leaves and petioles of D. leichhardtii have previously only been reported on the leaves of D. innoxia (Timmermann, 1927a; Haller, 1946; Karkoszka, Krasowska and Rogoyska, 1957; Verzár-Petri and Sárkány, 1961) but they are common on corollas (Santos, 1927; Wallis and Rohatgi, 1952) and we have observed them on young seedlings of D. stramonium. The stomatal index of the leaves of D. leichhardtii, when compared with published values for D. stramonium, D. innoxia and D. metel (Rowson, 1946; Košová and Chládek, 1957; Verzár-Petri and Sárkány, 1961) would seem to be of little value for differentiation. Similarly the palisade ratio is within the general range for the genus and the stomatal number ratio, although different from D. innoxia is similar to that of D. stramonium (Timmermann, 1927b). In thickness the lamina is similar to D. stramonium and D. metel but thinner than D. innoxia (Timmermann, 1927a). A tendency towards the formation of prismatic crystals of calcium oxalate in the collecting layer of leaves of D. leichhardtii can serve as a useful distinguishing feature but this characteristic is variable and cluster crystals may predominate. The only other species of *Datura* in which prismatic crystals



FIG. 7. Datura leichhardtii Muell. ex Benth. A, transverse section of midrib at location A3, Fig. 5. B, longitudinal section through petiole at right angles to the plane of symmetry. Both \times 180. a, starch; col, collenchyma; c.t, clothing trichome; cu, cuticle; ep, epidermis; e.ph, external phloem; *i.ph*, internal phloem m.x, metaxylem; par, parenchyma; pr.x, protoxylem; s.x. sandy crystals of calcium oxalate; x, xylem.

of oxalate have been cited as the main type is D. discolor (Kalemkiarian and Miller, 1957) but leaves of this species, raised in Nottingham, have consistently contained cluster crystals.

The structure of the transverse section of the stem closely resembles that of *D. stramonium* (Fischer, 1937).

Summary of Microscopical Characters

The principal features of the microscopy of the leaves and stems of *D. leichhardtii* are:

1. An upper leaf epidermis having cells with almost straight anticlinal walls and possessing mainly anisocytic stomata. A lower epidermis with wavy anticlinal walls and about twice as many stomata. The cuticle of neither epidermis is striated.

2. Leaf trichomes are of three types: small clavate glandular trichomes of the type found in all the examined species of the genus; a limited number of glandular trichomes possessing a uniseriate stalk and a single-celled head; covering trichomes, uniseriate and 1 to 4 celled, with warty walls and commonly 125 to 200 μ in length.

3. A collecting layer of cells in the leaf lamina containing prismatic or cluster crystals of calcium oxalate or both.

4. The structure of the midrib resembles that of other members of the genus as does that of the stem. The lignified wood elements of the latter include vessels, fibres, wood parenchyma and medullary rays. Internal and external phloem are present; fibres are associated with the internal phloem and slightly lignified fibres indicate the pericycle.

5. Sandy crystals of calcium oxalate occur as idioblasts in the parenchyma of the stem, petiole and midrib.

6. Palisade ratio, stomatal index and stomatal ratio are of little value for distinguishing *D. leichhardtii* from other members of the genus.

The similarity of these characters to those of some other species of *Datura* renders the identification of *D. leichhardtii* in the powdered form difficult. The anatomical features of the leaves which collectively serve to distinguish the species are: the occurrence in some samples of many, and often a predominance of, prismatic crystals in the collecting layer of the leaves, relatively few clothing trichomes on the leaf surface compared with most other members of the Section Dutra, and the presence of glandular trichomes with a uniseriate stalk and a single celled head.

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