Bio-histological notes on some new Rhodesian species of Fuirena, Hesperantha, and Justicia.

BY

L. S. GIBBS, F.L.S.

With Plates XI and XII and ten Figures in the Text

IN a former paper [1] some points of biological interest in connexion with the above plants collected by the author in Southern Rhodesia were briefly touched upon. The results of further investigation are now given in greater detail, and show very marked adaptation to physiological conditions, which in the case of *Fuirena Oedipus* and *Justicia elegantula* have resulted in types of peculiar specialization quite outside the known limits of their respective families.

On the high Matabeleland plateau of Southern Rhodesia the rainfall varies from 17 to 30 inches, occurring chiefly in the form of thundershowers, and it is entirely limited to the summer or hottest months of the year, when evaporation is greatest. The general altitude is 3,000–4,500 feet, with a mean annual temperature of 65° to 70° and five absolutely rainless months in the year. In a tropical country of this description the rainfall is sufficient to support a stunted growth of trees, many shrubs, and herbaceous plants. These meet the extreme conditions to which they are exposed rather by husbanding the general underground water supply in the soil than by elaborating individual forms of water reservoirs. Water storage tissue seems more characteristic of regions of slight intermittent rain and short periods of surface moisture.

The long seasonal winter drought, with cold nights and hot days, is met, in the case of trees, by the throwing off of leaves and by a great variety of cork protection. The efficiency of this enforced quiescence is proved by the fact that the severe frosts which sometimes occur at this season leave the native vegetation untouched, though they are often injurious to introduced trees and shrubs.

Herbaceous plants have evolved most massive underground root systems, and if they do not die down every year they are cut back by the veld fires. The aerial parts are characterized either by a flat spreading habit

[1] Gibbs, A Contribution to the Botany of Southern Rhodesia. (Journ. Linn. Soc., xxxvii, 1906, pp. 426–94, Pls. XVII–XX.)

or by an extreme leaf development, or the specialization of vegetative shoots which succeed the earlier flowering ones. These secondary vegetative shoots, as well as many herbaceous and other plants with soft woody stems, show a decumbent tendency, ultimately spreading on the ground. Striking organographical deviations to meet physiological conditions are conspicuous by their absence, and this fact is no doubt due to the sufficiency of underground moisture which can be drawn upon as required. The limitation of that supply, however, is shown by the strict economy exercised in its distribution. The characteristic spacing of trees, already referred to [1], is reproduced in the growth of herbaceous plants, and may probably be referred to this factor. Each plant whilst exhausting the water supply in its own vicinity tends to crowd out other competitors by extending its shade area, and thus exercises, possibly as a secondary result, a retarding influence on evaporation.

This bare sufficiency of soil moisture is apparent in the general beginning of plant life in September and October, before the rains. The rigid economy necessitated by the limit of that supply is seen in the tendency of trees and shrubs to flower before the leaves expand, and this habit is further modified in herbaceous plants by the development of specialized flowering shoots. In this way the whole energy of the plants is centred on vegetative activity only during the short season favourable to growth.

The bulbous annual tender herbaceous plants are apparently restricted to the summer or rainy season. The few species of *Crinum*, *Buphane*, *Albuca*, *Urginea* and *Gladiolus* which signal the early spring invariably send up the flowering scapes first, even the fruit maturing before the leaves appear; but in the case of bulbs of *Albuca caudata* Jacq. and corms of *Gladiolus Melleri* [2] brought back by Baker this habit has proved to be due to biological conditions. Under favourable cultivation both flowering scape and leaves have been simultaneously developed. The same remarks apply to trees and shrubs found growing under varying conditions in their natural surroundings.[3] The *Fuirena* and *Justicia* species here described would thus prove exceptional to the general rule, being characterized by very distinct organographical modification which takes the form of starch storage tissue, in the former a portion of the stem, and in the latter special leaves, being involved in its elaboration. In both examples, however, this specialization is not to meet the long physiological drought conditions of widely different edaphic character (*Fuirena Oedipus* being a hygrophilous and *Justicia elegantula* a veld-type) to which each plant is exposed, but to ensure sufficient reserve food supplies to promote a rapid spring growth, with the least expenditure of energy.

[1] Gibbs, l. c.

[2] This case is particularly interesting, as the corms were given to Dr. Bolus at Cape Town and grown out of doors. The first time the plant flowered, the foliage did not come up till two months later, but the second year both scape and leaves came up together.

[3] Gibbs, l. c.

FUIRENA OEDIPUS C. B. Clarke.

The aerial shoots of this species are about 20–40 cm. high (Pl. XI, Fig. 1), and these arise at more or less regular intervals on the horizontal rhizome. The stem is four-angled, but the basal node of each aerial shoot is modified in the form of a round sessile pseudo-bulb with contracted base. These swollen internodes when collected were white and gleaming with a smooth surface, and are very apparent as they burst through the brown membranous scale-leaf of the node. The basal nodes are most developed in the flowering shoots of the current year (Fig. 2, *b.i.*) where they are globose in shape. In the vegetative shoots they are more elongated (Fig. 1); while in the dead shoots of the previous year, having given up all their reserve food material, they have shrunk both to the quadrangular shape and to the usual proportion of the stem (Fig. 1, *d.s.*). The plant was found at the Victoria Falls in September, growing in what, in a previous paper[1], is described as the bog edge of the so-called Rain Forest. This bog edge consists of a zone of hygrophilous plants, varying in width and plant association, both apparently being determined by the intensity of the spray-fall from the cataract on the opposite side, during and after the rainy season, when the Zambesi is in flood. The river then falls in one sheet of water over its whole width, and the spray, which has been measured by theodolite to reach the height of 3,000 feet, is continuous and may be described as perpetual rain. When this plant was in flower, the river was almost at its lowest, reduced to about four separate falls. It was found growing almost opposite to the Devil's Cataract, where only grasses and sedges formed a tangled mass. The spray at that season falls intermittently as a fine mist, according to the direction of the prevailing breezes. The foliage was sometimes dry, but generally a dew-like moisture rested on the leaves, notwithstanding the continuous sunshine above.

As might be expected from such surroundings, the plant is very hygrophilous in habit, the upper leaves showing long and broad laminae, while the scale leaves of the lower stem-internodes, and of the rhizome, are quite membranous in texture and not persistent. These facts, considered with the histological examination, agree with the results of other workers on the Gramineae and Cyperaceae, where biological conditions in relation to habitat have been taken into account[2]. Unfortunately investigation was limited to the type specimen, which increased the usual difficulties in dealing with herbarium material.

HISTOLOGY

Rhizome. The rhizome is small, about 2 mm. in diameter throughout, with short internodes. It is covered with brown scale leaves, in the axils

[1] Gibbs, l. c. [2] Spinner, L'anatomie foliaire des *Carex* suisses, 1903.

of which the aerial shoots arise from a bifurcation of the rhizome. The branching is sympodial, and several aerial stems are given off in one season, both flowering and vegetative (Pl. XI, Fig. 1). The rhizome consists of a solid central cylinder (Pl. XII, Fig. 8) composed of many fibro-vascular bundles embedded in fundamental tissue: it is bounded by an endodermis accompanied by several layers of sclerotic cells (Fig. 8, *e. sch.*). A very broad cortex of unmodified parenchyma succeeds the endodermis and the sclerotic zone. Of this the peripheral portion is composed of larger cells, is not aerenchymatous, and is reinforced by hypodermal ribs and small isolated groups of more centrally placed sclerotic tissue (Fig. 8, *sch.*). The epidermis is slightly cuticularized, and tannin is abundant through the rhizome where starch occurs in the cortex, but not in the central cylinder. The cortex in the Cyperaceae, according to Plowman [1], is highly susceptible to environment and varies in the same species. Duval-Jouve [2] observes that in hot and damp localities in Algeria the cortical zone is soon destroyed, but persists longer in dry and sweet ('frais') places. He mentions this fact against Guillard's [3] theory that the size of the cortical envelope of roots and rhizomes depends on the humidity of the soil and not on a special organization. The present case would seem to support the latter author.

In the central cylinder the fibro-vascular bundles come under Plowman's [1] 'amphivasal' type, the bundles being concentric with the xylem distributed round the phloem (Pl. XII, Fig. 8, *a.v.b.*). The bundles are very numerous, especially near the periphery of the central cylinder. The central strands are larger, characterized by a large centripetal mass of sclerenchyma showing protoxylem lacunae. The section Plowman [1] describes and figures for *Scirpus cyperinus* Kunth might pass for *Fuirena Oedipus*, with the exception of the sclerotic ring round the endodermis, which, according to him, is characteristic of *Fuirena*.

Aerial stem. In this species the stem is quadrangular, as is also the case in *F. umbellata* Rottb.,[4] but otherwise this seems to be a very uncommon feature in the Cyperaceae, in which the stems are usually round or triangular. The first three or four internodes of the stem are very short and covered by membranous scale leaves, light brown in colour. A cross section through the third internode from the rhizome shows a typical hygrophilous structure (Pl. XII, Fig. 11) with large medullary air-spaces of schizogenous origin, separated by delicate plates of parenchyma which accompany the medullary bundles. The cortical bundles are arranged

[1] Plowman, Comparative Anatomy and Phylogeny of the Cyperaceae (Annals of Botany, xx, 1906, pp. 1–33, Pls. I–XI).

[2] Duval-Jouve, Étude histotaxique des *Cyperus* de France (Mémoires de l'Acad. des Sci. et des Lett. de Montpellier, viii, 1874, pp. 347–412, Pls. XIX–XXII).

[3] Guillard, Bull. Soc. Bot. de France, xvi. 420.

[4] Rickli, Beiträge zur vergl. Anat. d. Cyperaceen, m. besonderer Berücksichtigung d. inneren Parenchymscheide (Pringsh. Jahrb. f. wiss. Bot., xxvii, 1895, pp. 485–580, Pls. XVIII–XIX).

regularly on the periphery, each accompanied by a hypodermal strand of fibres alternating with large lysigenous air-spaces (Fig. 11). Tannin sacs are present, and starch is massed in the two or three layers of parenchyma (Fig. 11, *t.s. st.*) which occur between the phloem and the hypodermal strands of fibres accompanying the cortical bundles. No starch was found in the sheath of colourless cells which surrounds each bundle. In this section the epidermis is without stomata, is thinly cuticularized, and its cells are smaller over the hypodermal ribs.

Basal internode. As has been already described, the lowest internode of the aerial stem is curiously modified for starch-storage purposes, and its form is due to a proliferation of the cortical tissue of the internode. The cross section is circular (Pl. XII, Fig. 9), the lysigenous air-spaces of the aerial stem being quite suppressed, though the sclerenchymatous ribs are still present, and the cells of the epidermis are smaller where they pass over them. The cortical bundles are pushed more towards the centre, showing that it is the starch-containing layers of parenchyma already indicated in the aerial stem (Pl. XII, Fig. 11, *st.*) which are responsible for the reserve storage tissue of the pseudo-bulb formation. Small schizogenous air-spaces occur freely in the cortex, and increase in size towards the medulla (Fig. 9), which is identical in structure with that of the unmodified portion of the stem (Fig. 11). All the cells, including those of the thin medullary plates of parenchyma, are densely packed with starch, resulting in a structure of corm-like consistency, the rigidity of which is due entirely to its stores of reserve material; the mechanical thickening, notwithstanding the great increase of surface, being no greater than in the upper portion of the stem. Tannin sacs are very numerous in the cortical region.

In longitudinal section (Pl. XII, Fig. 10) the subtending leaf-trace bundles are seen to insert themselves on the cortical bundles of the stem at each node (Fig. 10, *l.t.b.*) essentially as figured by Plowman [1] for *Dulichium arundinaceum* Brit., and the arrangement is similar in the basal node, in which the reserve food tissue is strictly limited to the proliferation of the cortical parenchyma.

Examples of special organogenic modifications for the storage of reserve food material are of exceptional occurrence in the Cyperaceae, and, as far as investigation goes up to the present, are entirely limited to the rhizome. Holme [2] has recorded for *Fuirena squarrosa* Michx. a tuberous development of one of the internodes of the rhizome, which takes the form of a shoot with the growing point arrested, the tissue composing it being packed with starch. He cites this case as being very rare in the genus, comparing it with the tuberous rhizome of *Cyperus esculentus* Linn. and *C. Rhymatodes* Muhl. described by Duval-Jouve [3] as being formed from

[1] Plowman, l. c.

[2] Holme, Studies in the Cyperaceae (Am. Journ. Sci., 1897, pp. 13-25, Pls. 1-2). [3] Duval-Jouve, l.c.

several internodes which, at the point where the rhizome bifurcates in the formation of the aerial stem, instead of elongating like the others, remain short and swell to a considerable size, the rest of the rhizome being slender and wiry. In grasses, tuberous swellings involving the lowest internodes of the culm and foliage-shoots (Knollen-Gräser) or the base of the leaf-sheaths (Zwiebel-Gräser) are common. According to Hackel[1] these are characteristic of species inhabiting regions of periodical drought, where they serve as water reservoirs, he having never found any reserve material in them, at whatever season examined.

The late Mr. C. B. Clarke, whose knowledge of the Cyperaceae was unrivalled, was much struck by this plant, to which he gave such a peculiarly appropriate specific designation. A similar modification was unknown to him in the order.

The leaf. In this species the lamina is 6–7 mm. broad, 15–18 cm. long, with five prominent nerves on the dorsal side, corresponding to the same number of grooves on the ventral surface, which is covered with unicellular hairs, such as, according to Rickli[2], are typical of *Fuirena.*

The structure of the leaf is very interesting owing to the extreme differentiation of the epidermis on the ventral surface, the cells composing it being thin-walled and enormous in size. (Pl. XII, Fig. 12, *v.e.*)

As the genus *Fuirena* has been hardly touched upon in work on other families in the order, sections were cut of the leaves of two other species collected in the same season in the Matoppo Hills, but found growing under different conditions and showing a more xerophytic habit. For purposes of comparison these are now described.

Fuirena stricta Steud. A plant of very wide distribution throughout tropical Africa and the Mascarene Islands. It was growing in a bog, in probably a stagnant and acid substratum. The stem is triangular, with very long internodes almost covered with nearly equally long leaf-sheaths, the laminae of which are very much reduced, being narrow and very short. The scale leaves of the rhizome and the lower stem-internodes are membranous. In this case the cells of the epidermis on the ventral surface of the leaves are large. *Fuirena subdigitata* C. B. Clarke[3] shows a more hygrophilous habit, but the structure of the leaves is very xerophytic in type. The laminae are considerably longer than the encircling leaf-sheaths. The stem is triangular, with long internodes not entirely covered by the leaf-sheaths. This plant was growing on damp sand-banks in a stream, the roots therefore in moisture, while the aerial shoots would be exposed to powerful illumination. The scale leaves are in this case very hard and persistent, possibly to withstand the effects of inundation in the rainy season.

[1] Hackel, Ueber einige Eigenthümlichkeiten der Gräser trockener Klimate (Verhandl. Zool.-Bot. Ges. Wien, 1890, pp. 125–136).

[2] Rickli, l. c.

[3] Gibbs, l. c., p. 477.

The epidermis. Cuticularization is not very pronounced, showing little reaction to iodine or sulphuric acid, but the area of the cuticle is increased by papillary outgrowths of hammer-headed form (Pl. XII, Fig. 14). This 'granulation,' as Rickli[1] calls it, has been described by various authors and considered typical of hygrophilous species in the order. Rickli found that it varied in the same species and was limited to the neighbourhood of the stomata, and, as these lie in channels, water and rain could follow the depressions and so swamp the apertures. The granulation, he surmised, would hold the water and so prevent the temporary cessation of stomatic function. Possibly it might have that effect and in some species may be more pronounced in the vicinity of the stomata, but in *F. Oedipus*, where it is particularly well developed, and in the other species examined, it occurred over the whole surface of the leaf, which on the vertical side is devoid of stomata. In the former the cuticle of the stem, with the exception of the basal node, shows the same peculiarity.

The stomata consist of four cells of the usual type limited to the Gramineae and Cyperaceae (Pl. XII, Fig. 14 *a*), the mechanical structure of which has been very thoroughly worked out by Schwendener.[2] In considering the position of the stomata he states that in the representatives of steppe and desert flora they are sunk, but this condition is also found in the inhabitants of boggy places. The latter point is brought out in rather a striking manner in the present case, the stomata showing different positions in each of the three species collected, though all might be ascribed to the above habitat. In *F. Oedipus*, where the aerial stem is usually bathed in moisture, the stomata are raised above the surface of the epidermis (Pl. XII, Fig. 12), possibly ensuring more rapid transpiration, which cannot go on where the surrounding atmosphere is saturated with water-vapour, but perhaps also the position may serve to check the lodging of films of water across the orifices of the stomata. In *F. sub-digitata*, where the rhizome alone is in perpetual moisture and the aerial shoots are exposed to full light and heat conditions, the stomata are not only sunk, but the cuticle of the guard-cell is produced into four papillae which project across the opening, almost covering it. This is precisely what Volkens[3] has described for some Carices growing in similar situations, notably *C. panicea* Linn. The flooding during the rains to which *F. sub-digitata* must be subjected may also account for this development of the stomata, which in *F. stricta* are only slightly sunk and not provided with protective covering, though found growing in a bog medium liable to desiccation.

The cells of the epidermis throughout the Cyperaceae show distinct

[1] Rickli, l. c.

[2] Schwendener, Die Spaltöffnungen der Gramineen u. Cyperaceen (Sitzungsb. K. Akad. Berlin, 1, 1889, pp. 65–78, Pl. I).

[3] Volkens, Zur Kenntniss der Beziehungen zwischen Standort u. anat. Bau der Vegetationsorgane (Jahrb. Bot. Gart. Berlin, iii, 1884, pp. 1–46, Pl. I).

differentiation on each surface of the leaf, those on the dorsal surface being much smaller than those on the ventral or upper side. The contents of all the cells are colourless, and only the outer walls are thickened, the radial and inner tangential walls being of an extremely delicate texture.

On the dorsal surface they are smaller over the hypodermal ribs (Pl. XII, Figs. 12 and 13), where the development of the hard fibrous cells seems to arrest their radial expansion, which is shown in a transverse section through a developing leaf of *C. stellulata* Good (Fig. 15). In the youngest stage obtainable, the sclerenchymatous cells not having yet differentiated out, those of the epidermis are still more or less equal in diameter. The peculiar cone-like base limited to the most radial of these cells noted by Duval-Jouve [1] in *F. pubescens* Poir. was not seen in the species examined. The ventral epidermis is marked by enormous thin-walled cells with colourless contents (Pl. XII, Figs. 12 and 13). The outer walls alone are cuticularized together with the unicellular hairs which are scattered over its surface, the radial and inner tangential walls are very delicate in texture. These cells in the vicinity of the vascular strands are radially elongated, and there is always an intimate connexion with the bundle-sheath of delicate thin-walled cells (Figs. 12 and 13). This connexion is continuous with the dorsal epidermis by means of small colourless cells passing up both sides of the sclerenchymatous ribs which accompany the bundles on that side.

The large cells which occur in groups in the epidermis of grasses, and throughout the Cyperaceae, characterize the entire ventral epidermis of the leaf in varying degrees of differentiation, and have been described as 'bulbiformes' by Duval-Jouve, who observed that stomata were always absent on a 'bulbiforme' epidermis. Tschirch [2], who looked upon them as characteristic of steppe and meadow grasses, gave them the name of 'Gelenkzellen', as he considered they controlled the folding and unfolding of the leaves of grasses by their turgescence or loss of water. Volkens [3] states that he has never observed the folding up of the lamina of a grass leaf, but always a windbag (Blasebalg) action, as the lamina increases or decreases in width according to the turgescence (Wasserzufuhr) of these cells, which proves they function as a water reserve. He therefore rechristened them 'Wasserzellen'.

Rickli [4], noticing the delicate radial and inner tangential walls of all the epidermal cells, looks upon the whole organization as a water-jacket, and there can be no doubt that this interpretation is correct. This is shown by the connexion, between the two surfaces, with the bundle-sheaths, as already pointed out, by the delicate inner walls, and by the limitation of the stomata

[1] Duval-Jouve, Sur une forme de cellules épidermiques qui paraissent propres aux Cypéracées (Bull. Soc. Bot. France, xx, 1873, pp. 91–95).

[2] Tschirch, Beiträge zu der Anatomie u. dem Einrollungsmechanismus einiger Grasblätter (Pringsh. Jahrb., xiii, 1882, pp. 544–68, Pls. XVI–XVIII).

[3] Volkens, Flora der ägyptisch-arabischen Wüste, 1887.

[4] Rickli, l. c.

to the dorsal side, which allows of a larger size of the water-jacket cells on the ventral or exposed surface. This fact, coupled with the entire absence of extreme cuticularization and hairy covering in the order, shows the adequacy of this simple protection.

As Rickli [1] expressly dwells on the delicate and radially stretched walls of the ventral epidermis of *Fuirena scirpoidea* Mich., *F. repens* Kth., it was suggested that the development of this tissue, so conspicuous in *F. Oedipus*, might be a special character in the genus, but examination of the other species available did not bear out this hypothesis.

In *F. sub-digitata* these cells are about the same size and shape as in many species of *Scirpus*, *Cyperus*, and *Carex*. In *F. stricta* they are larger and radially elongated, but not so conspicuously different as in *F. Oedipus*. In both species, however, the connexion with the bundle-sheath is very well marked, especially on the dorsal side, where the hypodermal ribs are better developed than in *F. Oedipus*, and the connecting colourless cells, which break away from the sheath and run up each side of the fibrous groups, are more numerous and larger in size.

The larger area of leaf surface in *F. Oedipus*, coupled with the organization of the stomata for rapid transpiration, no doubt necessitates the reinforcement of the water-jacket on the exposed ventral surface. It is the only organization for the protection of the palisade tissue, and the very marked increase in the size and volume of the cells proves what a very efficient as well as plastic organization such an uninterrupted water reservoir must be.

Palisade and mesophyll tissue. The former is well differentiated (Pl. XII, Fig. 12), a fact, according to Plowman [2], rare in the Cyperaceae, but also seen in *F. stricta* and *F. sub-digitata*. It is composed of one layer and shows a decided convergence towards the bundle-sheath (Figs. 12–13). The *mesophyll* has a tendency to break down, forming the characteristic large lysigenous air-canals, which alternate with the bundles and are so typical of the order. Traces of diaphragms occur across these air-spaces in the mature leaf, but are composed of plates of mesophyll and show no approach to stellate form. In *Carex stellulata* these air-spaces were traced back, and it was only in the very youngest stage that the leaf tissue was found entire (Pl. XII, Fig. 15), and even then the area to be destroyed is marked by the larger intercellular spaces, resulting in a looser arrangement of the cells. In *F. sub-digitata* these canals are not present. They are replaced by large thin-walled cells with colourless contents, which show lateral connexions with the bundle-sheaths, and they no doubt reinforce the water-storage tissue of the leaf. The breaking down of parenchymatous tissue in this way may possibly be connected with rapidity of transpiration. In the stem the cortical parenchyma between the peripheral bundles is broken down, and in the leaves the mesophyll tissues are similarly affected.

[1] Rickli, l. c. [2] Plowman, l. c.

Areschoug[1] describes transpiratory parenchyma as distinguished by large lacunae, and where rapid transpiration is necessary the palisade tissue is reduced and the mesophyll increased. When transpiration is reduced, a system of water storage or palisade is elaborated. In *Fuirena sub-digitata* this result is obtained, and the air canals are replaced, through the whole length of the leaf, by water-storage tissue associated with stomata that are not only sunk but have their apertures partially covered over.

Vascular tissue. The vascular bundles are collateral. The phloem, directed towards the dorsal surface, is composed of small thin-walled cells with well-marked companion cells. A certain amount of starch is present in the phloem. The two vessels are always accompanied by a protoxylem lacuna and lignified parenchyma (Pl. XII, Fig. 12, *px. l.* and *l.p.*).

Bundle-sheaths. A sheath of large thin-walled parenchymatous cells, colourless in contents, surrounds each bundle (Fig. 12, *w.s.*), the water-sheath noted by Rickli[2] as occurring in many Cyperaceae. The inner 'Parenchymscheide' which the same author figures as characteristic of the Chlorocyperaceae, including *Fuirena*, was not observed in the species examined, though in *Fuirena stricta* a very well-marked sclerotic sheath of single cells surrounds each bundle inside the water-sheath. No starch was traceable in the cells of the latter, towards which the palisade cells show a marked convergence. The connexion with the epidermal water-cells provides an organization which surrounds all the vital parts of the leaf, not only reducing the temperature, but ensuring turgescence by eliminating transpiration on the most exposed surface. Thus protection against transpiration is effected by a very simple and, as we have seen, plastic organization, while other plants have to meet the difficulty by elaborate contrivances, involving much greater specialisation of structure, such as extreme cuticularization or collenchymatous thickening of the epidermal walls, secretion of mucilage, or hairy coverings.

The anatomical characters of the three *Fuirenas* examined are thus seen to be considerably modified by their environment, though from a general point of view their organization is on the well-marked developmental lines common to all the genera of the order. In *Fuirena Oedipus* the plant provides for a short and rapid growth-period by laying down starch reserves in the basal node of the stem. This is an advance in organization to storage in the rhizome, as it not only ensures the supply being further removed from the constantly wet substratum in which roots and rhizome lie, but also provides a short cut when the plant starts into growth, as the starch has not to be transferred from the rhizome to the aerial tissues. In the structure of the leaves, the hygrophilous habit is shown in the breadth and length of the lamina, also

[1] Areschoug, Der Einfluss des Klimas auf die Organisation der Pflanzen, insbesondere auf die anatomische Struktur der Blattorgane (Engler's Bot. Jahrb., 11, 1882, pp. 511–526).

[2] Rickli, l. c.

in the unprotected stomata, which suggest a shade habit. The hereditary organization of the plant, which enables it to form the epidermal water-jacket and dorsal stomata, has proved sufficiently plastic to meet altered conditions. Aerial exposure to intense illumination and intermittent dryness is made possible by materially increasing the size and volume of the water-cells on the exposed surface of the leaf, and a satisfactory adaptation to present environment is thus secured.

Where the aerial stem bears rather broad leaves with moderately well-developed lamina and is exposed to constant xerophytic conditions, we find the modifications more complete, and in *F. sub-digitata* we get the protected and sunk stomata and an increase of water-tissue which replaces the air-canals. In *F. stricta* on the contrary, where the leaves are fewer and the laminae very much reduced, beyond a slight sinking of the stomata and the reinforcing of the water-sheath by a strong sclerotic one, the hereditary organization of water-jacket and papillose cuticle has proved sufficient.

HESPERANTHA MATOPENSIS Gibbs.

This Iridaceous species was found growing amongst grass on the sandy banks of a stream, which had cut a channel through the sand a metre below the level of the veld. It was in flower and leaf in September, before any rains had fallen, after a period of five months' drought. The flowering scape was on a level with the surrounding yellow grass haulm, which the flowers, that only opened at night, rather resembled in their light straw-brown colour. Towards evening the perianth segments would reflect, exposing the style and stamens, and a delicate perfume was emitted.

The interest of the plant centres in the extraordinary development of the tunics in comparison with the minute size of the corm to which they act as a protective covering. The corms with the tunics are from 12 to 15 cm. long and 14–18 cm. broad; but the actual corm itself only measured 5 mm. in length and 8 mm. in breadth, the difference in size being accounted for by the old scale-leaves of each year's successive growth persisting as rings one inside the other, round the corm.

The morphological development of these scale-leaves, of which one only is produced every year, is very interesting and obtains throughout this genus and the allied genera of *Lapeyrousia* and *Geissorhiza* in varying degrees of complexity, but *Hesperantha matopensis*, as compared with material in the British Museum and at Kew, apparently shows the most extreme form.

The scale-leaves are symmetrical in form, flattened at the base, dark brown in colour, and of a hard, smooth consistency. They are split about a third of their length into longitudinal segments with laciniate margins (Text-fig. 1, *t*) due to a folding of the scale-leaf tissue, the split occurring up the centre of the fold. At the base round the flattened portion of the scale a horizontal fold occurs, and there the young corms break through, the two margins being gradually pushed apart by the growth of the cormlets (Text-fig. 2, *yg.c.*), leaving the same laciniate margins as on the longitudinal segments. The peltate base of the tunic then separates off as a round scale (Text-figs. 2 and 3, *p.b.*) while the upper portion remains as a persistent ring round the neck of the corm (Text-fig. 1, *t.*). In Text-fig. 4, where the base of last year's tunic has been removed, the young corm in its axil is seen resting against the base of this year's scale-leaf. In specimens of *H. matopensis* collected three to four of these rings only were

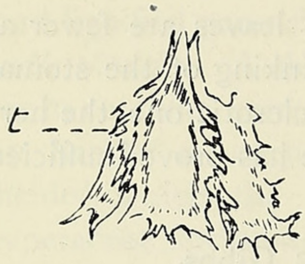


Fig. 1.

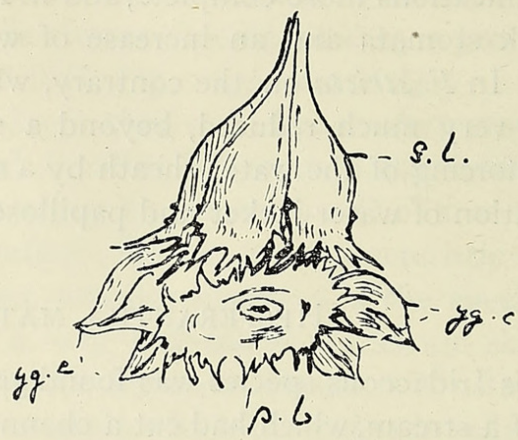


Fig. 2.

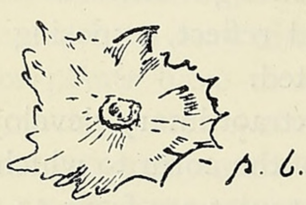


Fig. 3.

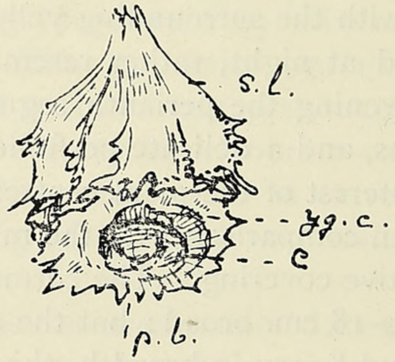


Fig. 4.

Hesperantha matopensis.

counted, but in a specimen of *H. falcata* Ker. Gawl. (Brit. Mus.) as many as eight scales were seen, occurring one above the other.

The tissue of the scale-leaf is composed of several layers of parenchyma, the inside layers of which lignify, while the outer ones remain membranous and form a white skin on both surfaces. The laciniation of the margins is caused by the splitting of the scale-tissue (a section through one of these teeth as shown in Pl. XII, Fig. 17, *l.p.*). Faint vascular strands consisting of one or two vessels run longitudinally down the scales, but are of no account in the development; the dark-brown colour is due to some form of colouring matter, not tannin, which only dissolves out after a week's soaking in Eau de Javelle. In a longitudinal section through a corm (Fig. 7) it will be seen that the folding of the scale-tissue which results in the longitudinal segments of the mature tunic is caused, like the basal scale, by the shape of the corm itself, which is furrowed ; it is these depressions which evidently induce the proliferation of tissue over their areas. The same proliferation occurs round the flattened base of the corm (Text-fig. 5, *h f.*) Text-fig. 6 shows the scale of a very young cormlet, still attached to the parent corm. In this stage the scale is entire, light yellow in colour, and membranous in consistency. The peltate base is indicated, following the shape of the cormlet, and the ridges already present in the latter have begun to form.

In comparing the tunics of *H. matopensis* with other species in the genus, a series is shown in the degrees of laciniation and the splitting of the margins, also in the longitudinal folding and the formation of the basal scale.

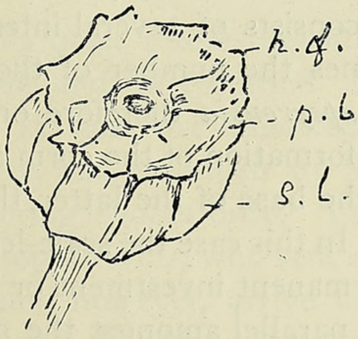


Fig. 5.

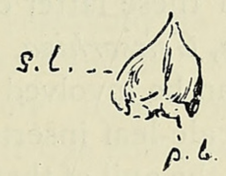


Fig. 6.

Fig. 7.

Hesperantha matopensis.

In *H. pilosa* Ker. Gawl., *Baurii* Baker, *candida* Baker, *lactea* Baker, and *falcata* there is no apparent peltate base to the tunics, the corm itself not being flattened, the tunics accordingly separate off at the actual base of the latter and the old persisting tunics consequently fit one above the other, each succeeding one being a little longer than the one which preceded it.

The tunics are also smooth with no foldings, following the round shape of the corm. In *H. radiata* Ker. Gawl. we see a slight beginning of the foldings and the peltate basal flattening, and this species amongst the British Museum specimens most approaches *H. matopensis* in tunic form.

Owing to the separation of the base of the scale from the upper portion in these species, the tunics remain apparently one inside the other, the difference in length not being so marked, as only the upper portion persists as a ring.

In *Lapeyrousia Sandersonii* Baker, *abyssinica* Baker, *erythrantha* Klotsch, and *coerulea* Schinz, the scale-leaf is the same as in *H. matopensis*. In *Geissorhiza* the base of the scale-leaves is not peltate, but breaks off from the base as in some species of *Hesperantha*, and in one species as many as ten superposed tunics, graduated in size, were counted.

In considering the morphological value of the scale-leaves of the corm of *Hesperantha* in comparison with other members of the order, there is very little literature to fall back upon. Irmisch [1] found that the corms of *Crocus*, *Gladiolus*, and *Romulea* are the product of the preceding year's activity of the plant and belong to an axis of a next lower order. As these dry up the basal internodes of the flowering axis thicken into fresh corms, which give up their reserve storage material to a new generation (Spross-Generation) next year. This year's corm has usually three scale-leaves, which are inserted on the base of the corm, but buds arise in the axils of the scale-leaves. In an earlier paper Irmisch [2], in considering *Crocus*, finds no transition between the scale- and the foliage-leaves, a short internode separating the uppermost scale-leaf and the lowest foliage-leaf. Both forms of leaf die off later, but the bases of the former remain as a protective investment to the corm, which in a moist climate is thrown off every year. As the thickened portion of the stem in these cases consists of several internodes, no doubt the number of these latter determines the number of the scale-leaves. In *Hesperantha*, *Geissorhiza*, and *Lapeyrousia* therefore only one internode of the stem can be involved in the formation of the corm and we get one corresponding scale-leaf inserted on the base of the latter, the next season's corms arising in the axil of that leaf. In this case the scale-leaf does not rot away, but lignifies, remaining as a permanent investment or tunic.

In this peculiarity we find an interesting parallel amongst the grasses. Hackel [3], in a paper on some peculiarities shown by the grasses of dry climates, enumerates so-called 'Tunika-Gräser' as showing protective scale-leaf investment according to their habitat. The grasses of the fertile meadows of Northern Europe and North Asia are characterized by delicate scale-leaves which soon decay, and only the remains of one or two are to be found in the base of the culm. In grasses from dry climates, on the contrary, these scale-leaves thicken and persist, and, according to the type of persistent thickening, may be divided into 'Stroh-Tuniken' and 'Faser-Tuniken'. The former develop into hard, often smooth, entire straw-like scales, while in the latter the soft parenchyma breaks down, leaving the bundles isolated. This type may be carried further in the 'Fasernetz-Tuniken' in which the bundles anastomose again, forming horizontal as well as longitudinal threads, and both these types of tunic investment, persisting, result in many layers over the base of the culms, protecting the young shoots. These tunics also serve to collect water, as the superposed layers hold it tenaciously. Having had occasion recently to look through the Tropical and South African genera of the Liliaceae, Irideae, and Amaryllideae, it was very striking to see that what Hackel

[1] Irmisch, Morpholog. Beobachtungen (Berlin, 1855, pp. 10–25).

[2] Irmisch, Zur Morphologie der Knollen- u. Zwiebel-Gewächse (Berlin, 1850, pp. 89–94 and 166–70).

[3] Hackel, l. c.

describes so well for the grasses is exactly paralleled in the protective tunics of the bulbs, corms, or rhizomes of the representatives of those orders in those regions. The 'Faser-' and 'Fasernetz-Tuniken' are perhaps the most common, but in some genera, viz. *Geissorhiza* and *Hesperantha*, abnormally thickened 'Stroh-Tuniken' only are found. In the latter case the membranous unthickened parenchyma surrounding the strongly lignified internal portion of each superposed tunic must effectively increase the sponge-like efficiency of the whole water-holding structure. This would be a very important point for a plant like *H. matopensis*, which has to compete for water, at the most inauspicious time of the year, with perennial plants, having abnormally well-developed root systems already in possession of, and in intimate relation with, the soil particles.

Justicia elegantula S. Moore.

This most interesting little plant is very widely spread in Southern Rhodesia and is recorded from Nyassaland as well (Nicholson, Herb. Kew). It was first collected by Dr. Rand in 1897 at Bulawayo and at Salisbury, and described by Mr. Moore[1] from those specimens, consisting of flowering shoots only. In 1902 it was collected again by Mr. Eyles in the Matoppo Hills, who sent a complete specimen to the British Museum; it did not, however, arrive until after the present investigation had been completed. In the present case[2] it was of very general occurrence in the Matoppo Hills, and a large quantity was noted on one of the sidings on the way up to the Victoria Falls, a fact which testifies to its wide distribution, though herbarium material is at present restricted to the specimens enumerated above.

The author first found it in August, growing in large patches on sandy veld, forming colonies suggestive of surface rooting origin. The little tufts of flowering shoots, scarcely a decimetre high, were dotted over these areas, where they were very conspicuous in the general deadness of surface vegetation, owing to their bright rosy pink flowers (Fig. 8).

Horizontally inclined, dead branches radiated from each tuft of flowering shoots (Text-fig. 8, *d.b.*). The latter, when taken up, were found to arise from winter resting buds of fleshy white radical leaves, forming sessile rosettes on a thickened rhizome beneath the surface (Text-fig. 8, *r.l.*). These rhizomes were not continuous, being limited to each group of shoots, and it was rather difficult to explain their origin. Finally, after some hunting, a vegetative shoot was found, with leaves still on it, which apparently explained matters, as it bore some roots at one of the nodes (Text-fig. 8, *n.r.*). On the flowering shoots the cauline leaves succeeding the hypogeal radical ones are at first small and linear, bearing

[1] Moore, Journal of Botany, XXXVIII, 1900, p. 204.

[2] Gibbs, l. c. p. 461.

the flowers in their axils (Text-fig. 8, *c.l.*). The radical leaves are minute, ovate-obcordate in shape (Text-fig. 9, *r.l.*). The first impression that they were water-storage organs was not borne out, as in section their tissues proved to be packed with starch. The structure is leaf-like (Pl. XII, Fig. 16), the palisade tissue being replaced by parenchyma in regular rows of cells on the dorsal surface (Pl. XII, Fig. 16, *p.*), while on the ventral surface typical mesophyll obtains, also packed with starch (Pl. XII, Fig. 16, *m.*).

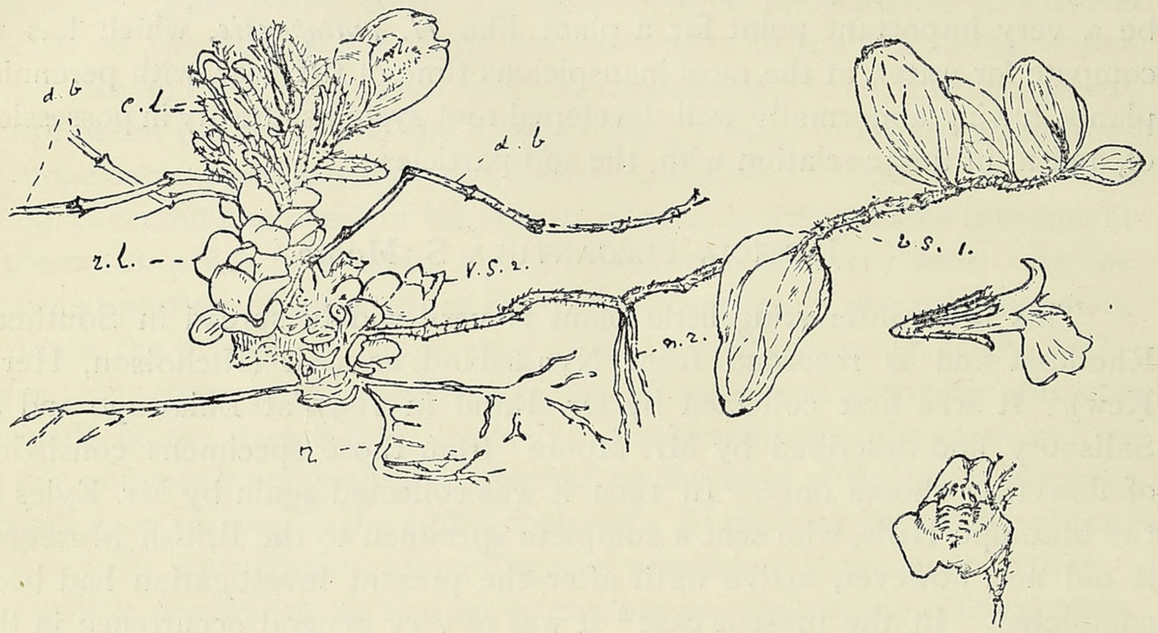


FIG. 8. *Justicia elegantula.*

Stomata occur on the epidermis (Pl. XII, Fig. 16, *st.*), which is cuticularized, and some multicellular hairs are seen in the central depression (Pl. XII, Fig. 16, *h.*). It was impossible to get a good section of the cauline leaves, though the fact was established that the bilateral structure is maintained in them. From Text-fig. 8, *v.s.* 2, it will be seen that several buds remain dormant on the rhizome, and it is no doubt these which subsequently break away later on in the season, growing out into the vegetative shoots already referred to (Text-fig. 8, *v.s.* 1.). These shoots rooting at the nodes (Text-fig. 8, *n.r.*), the thick rhizome is elaborated previous to the development of the resting buds on its surface. The leaves on this vegetative shoot are very large, ovate, and about 3 cm. long. From the material in the British Museum, kindly placed at my disposal for drawing, later stages in the development of the flowering shoots could be followed. In specimens collected by Dr. Rand in September and October, the flowering shoots had elongated considerably, and the cauline leaves increased in size, whereas in December the erect growth was already lost and the shoot had dropped into a horizontal

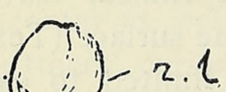


FIG. 9. *Justicia elegantula*, Radical leaf.

position, the cauline leaves showing a very considerable increase in size, though still linear in outline (Text-fig. 10). The whole shoot at this stage assumes a dorsiventral habit, the little axillary flowering shoots rising erect from each node. It is the remains of these decumbent flowering shoots which form the radiating dead branches in Text-fig. 8, *d.b.*, in which no trace of nodal rooting was observed either in the field or in the material brought back. The cauline leaves also in this case, though they increase so considerably in size, remain more linear than the ovate leaves on the purely vegetative shoot, on which there are no flowering axes to exhaust vitality. The later development of vigorous vegetative shoots brings this highly specialized *Justicia* into line with the general characteristic type of vegetative activity already referred to, by which plants requiring a long period of development economize their resources by taking the process in two stages. This habit is possibly stimulated in herbaceous plants by the annual veld fires, as it ensures a double chance in case of premature destruction of the purely reproductive shoots. That it forms the direct response to the prevailing climatic and edaphic conditions is shown by the wide adoption of the principle, in one form or another emphasized in the very early flowering of nearly all the trees, many shrubs, and those herbaceous plants and bulbs the organization of which calls for a large area of assimilating surface to elaborate next year's supplies. The decumbent shoots also form a very general adaptation, in this case peculiarly appropriate, for retarding evaporation, and ensuring a shade area at the stage when the winter buds are being laid down on the rhizome.

In its peculiar complexity of organization *Justicia elegantula* not only occupies an isolated position in its own genus, but

FIG. 10. *Justicia elegantula.*

also within the whole alliance. In the Acanthaceae tuberous development is very rare, and Lindau[1] only refers to *Ruellia tuberosa* as an example, in which case it takes the form of local swelling of the roots. The peculiar development of specialized leaves for nutritive purposes finds no parallel in this order, though rooting at the nodes is a general feature. The production of resting buds is well known in certain families, notably species of *Epilobium*, i. e. *E. parvifolium* Shreb., *E. montanum* Linn., and *E. lanceolatum* Sebast. et Maur, where the autumnal stolons produce fleshy white rosulate leaves, very similar in appearance to those occurring in the present case. Goebel[2] quotes *Androsace sarmentosa* Wall. as forming resting leaf rosettes consisting of leaves very different from the foliage-leaves. In *Utricularia* and *Myriophyllum* winter buds or turions are formed, but these examples serve also for vegetative reproduction, as they may be detached from the parent plant, which is not the case with sessile leaf rosettes, which are organs modified as reserved storage-tissue for the purpose of accelerating next year's growth.

In conclusion we may point out that in two plants of most widely differing organization and systematic position, exposed to the same physiological but rather divergent edaphic conditions, the direct response is on the same lines in both cases, and in the same direction, viz. to the general or physiological stimulus rather than to individual requirements. The important organogenic modifications involved are attained in both cases by the specialization of some organ or organs as a reserve food store, thus providing not for present requirement, but for future need. To ensure next season's rapid growth on the most economical lines, present opportunities are utilized to the utmost, but the necessity of elaborating contrivances to meet potential adverse circumstances represented by a prolonged physiological drought is discounted, and the plant secures itself against the periodic recurrence of dry seasons by the cessation of all vegetative activity in the annual dying down of its aerial shoots. It is the mean of physiological environment and not the extreme which here determines biological modification. In the case of *Fuirena Oedipus*, which was in flower in September, the favourable growing period would probably cease in January, when the summer rains begin to affect the volume of water in the river (p. 191). From then till June it would be exposed to a continual downpour, with its rhizome and roots in standing water. For *Justicia elegantula* the conditions are apparently different, though physiologically the same, as it is one of the few surface-rooting veld plants. Amongst these latter the absence of stolons or surface-rooting runners was very conspicuous, though a widely spreading system of dorsiventral shoots was such a very general adaptation. *Listia heterophylla* E. Meyer, on moist sand-banks near streams, roots very freely at the nodes, but the same plant on the veld shows a very

[1] Lindau, Nat. Pflanzenfamilien, iv. 3 b.

[2] Goebel, Organography of Plants, p. 398.

limited branching system and, as far as early spring conditions go, no tendency to nodal rooting. *Lobelia thermalis* Thunb., a plant of very wide South African distribution, but in this case only found growing over rocky banks by a stream, was a very free surface-rooter, sending the rootlets down between the fissures of the rocks. On the veld the absence of surface moisture is no doubt a deterrent to this habit, and *Justicia elegantula* has had to adapt itself to surface-rooting by so organizing its vegetative growth that the energies of the plant can be directed towards the elaboration of a tuberous rhizome, and on this the starch-packed radical leaves are laid down. The plant is therefore doubly ensured against the long drought and the accompanying absence of moisture in the sandy surface of the soil. That the results are successful, is well shown in the wide distribution of the plant already referred to (p. 201), and it may be put down as one of the commonest Rhodesian types.

Hesperantha matopensis calls for no further remark. The development of its corm-tunics is on lines common to tropical and South African bulbous plants, which, as Hackel has shown in the case of grasses, is characteristic of dry climates in general, and is correlated with the supreme necessity of ensuring a sufficient store of moisture round the roots and young shoots.

Finally, my thanks are due to Dr. Rendle, of the British Museum, for kindly placing material at my disposal, and to Professor Farmer for his advice and criticism in the course of this work.

ROYAL COLLEGE OF SCIENCE,
May 2, 1907.

EXPLANATION OF PLATES XI AND XII.

Illustrating Miss L. S. Gibbs' Paper on new Rhodesian Plants.

O. ovule. *r.* raphe. *v.b.* vascular bundle. *d.s.* dead shoots. *b.i.* basal internode. *sch.* sclerotic tissue. *e.* endodermis. *p.* plexus of bundles. *a.v.b.* amphivasal vascular bundle. *p.x.l.* protoxylem lacuna. *st.* starch. *t.s.* tannin sac. *l.t.b.* leaf-trace bundle. *c.b.* cortical bundle. *m.b.* medullary bundle. *b.h.* base of hair. *v.e.* ventral epidermis. *d.e.* dorsal epidermis. *a.c.* air canals *l.p.* lignified parenchyma. *w.s.* water-sheath. *m.* mesophyll. *p.* palisade. *st.* stomata.

PLATE XI.

Fig. 1. A portion of a plant of *Fuirena Oedipus* showing the rhizome bearing old and young flowering and vegetative aerial stems, the basal internodes of which are swollen, forming starch storage-tissue ; the old stems to the right show reduction in size owing to the resorption of the reserve material. Reduced.

Fig. 2. A flowering shoot detached from the rhizome.

Fig. 3. A flowering spikelet detached from the inflorescence. × 16.

Fig. 4. A flower in the axil of a bract. Mag.

Fig. 5. A fruiting bract. Mag.

Fig. 6. A flower showing the three perianth segments alternating with the three stamens, and the triangular ovary. × 75.

Fig. 7. A longitudinal section through the ovary, showing the erect anatropous ovule. × 75.

PLATE XII.

Fig. 8. Part of a transverse section of the rhizome of *Fuirena Oedipus*, showing the broad cortex with hypodermal sclerotic ribs, the endodermis reinforced by a zone of sclerotic cells, and the solid central cylinder with amphivasal fibro-vascular strands, more numerous towards the periphery. × 110.

Fig. 9. Part of a transverse section through the swollen basal internode, showing the prolifera- tion of cortical tissue for starch storage purposes, a peripheral ring of leaf-trace fibro-vascular bundles, an inner cortical ring, and the medullary bundles, which are connected by thin plates of parenchyma across the large air-canals of schizogenous origin of which the medulla is composed. × 65.

Fig. 10. A radial longitudinal section through the basal internode, showing the insertion of the leaf-trace bundles on to the cortical bundles, the limits of the starch storage cortical tissue, and the medulla with its large air-spaces. × 16.

Fig. 11. Half of the transverse section of the stem taken through the third internode from the base, showing the hypodermal ribs, cortical parenchyma reduced to two or three layers, which show starch contents where they pass over the cortical bundles, the latter alternating with lysigenous air-spaces, and a medulla identical in structure with that of the basal internode. × 110.

Fig. 12. Part of a transverse section of the leaf, showing the differentiation of the epidermal cells on the dorsal and ventral surfaces, the connexion of the water-sheath surrounding the vascular bundles of the epidermis, and the lysigenous air-spaces which replace the mesophyll tissue of the leaf. × 1000.

Fig. 13. Transverse section of half of the leaf, showing the stomata limited to the dorsal surface and the very large water-cells and unicellular trichomes on the ventral surface. × 75.

Fig. 14. Part of a longitudinal section of the leaf, through an air-canal, showing the breaking down of the mesophyll tissue and the papillose outgrowth of the cuticle of the epidermis. × 1000.

Fig. 14 A. Surface view of stoma.

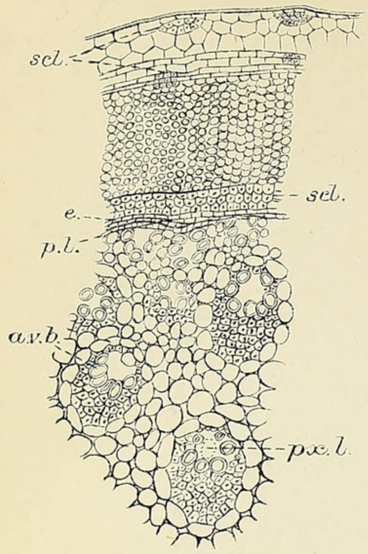
Fig. 15. Part of a transverse section through a developing leaf of *Carex stellulata* in the very youngest stage, showing the mesophyll tissue not yet broken down. × 1000.

Fig. 15 A. Part of a longitudinal section of a very young leaf of *Carex stellulata*, showing the mesophyll tissue beginning to break down. × 1000.

Fig. 16. Part of a transverse section through a fleshy radical leaf of *Justicia elegantula*, showing starch storage in its tissues. × 1000.

Fig. 17. A transverse section through one of the laciniate teeth of a scale-leaf of *Hesperantha matopensis*, showing the lignified inner layers of parenchyma.

GIBBS — RHODESIAN PLANTS.



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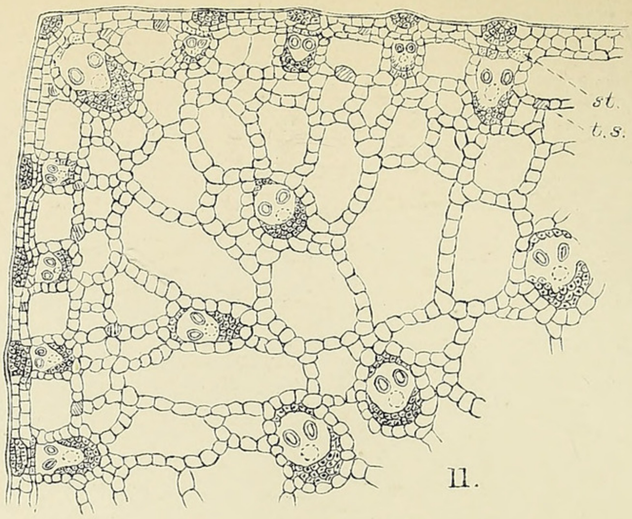

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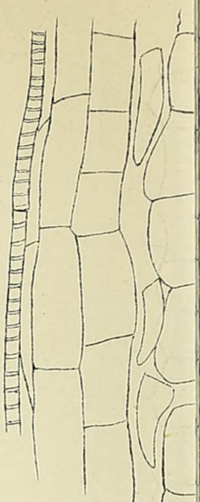

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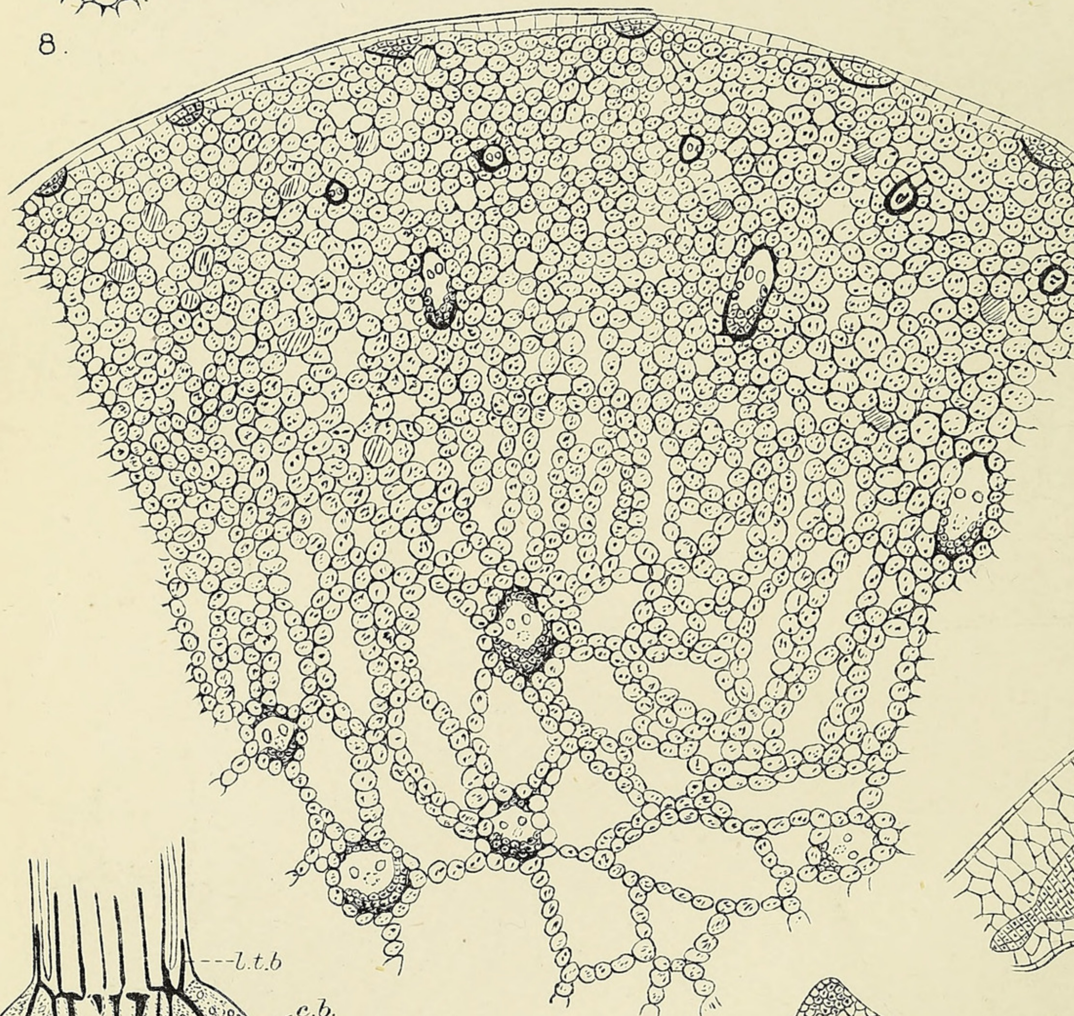

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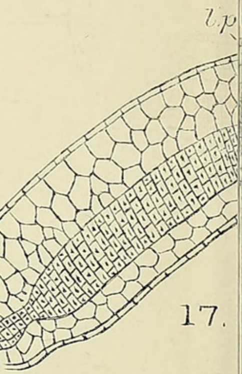

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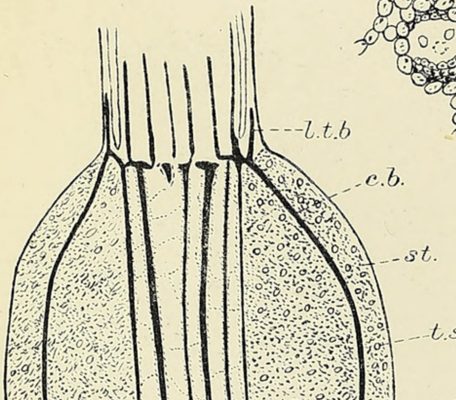

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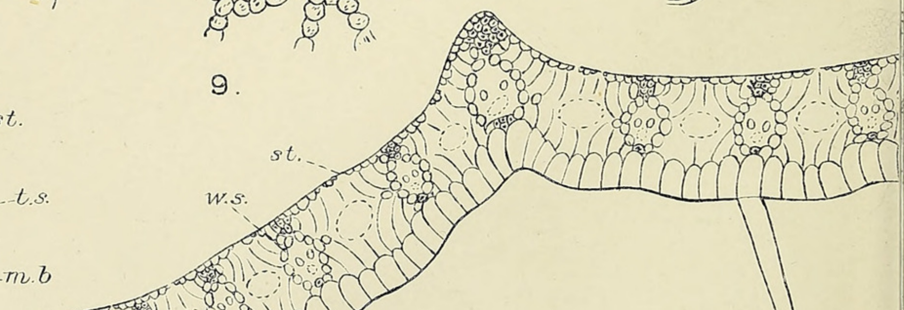

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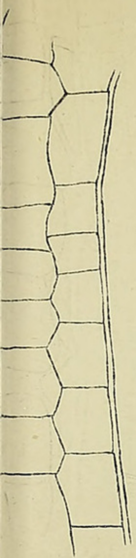

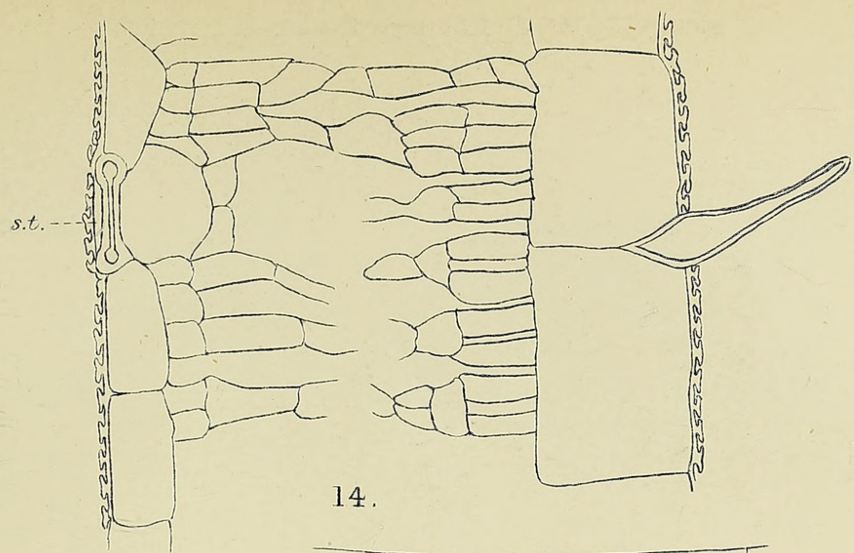

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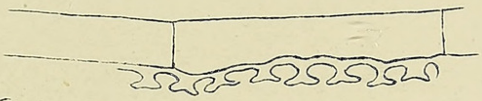

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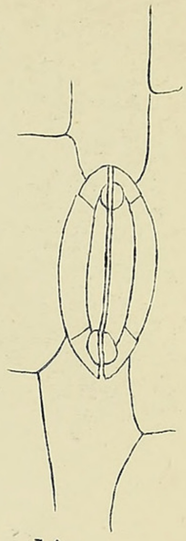

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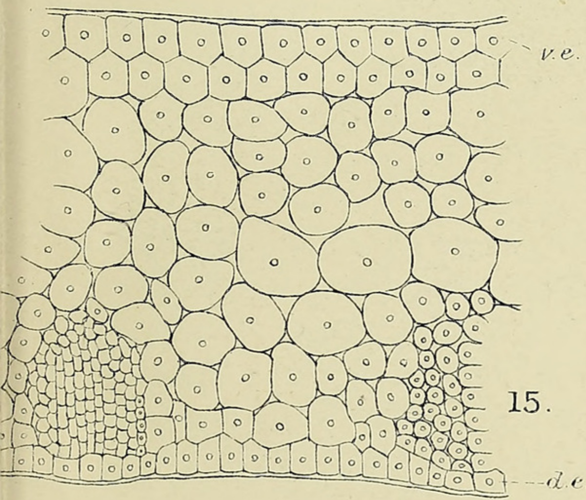

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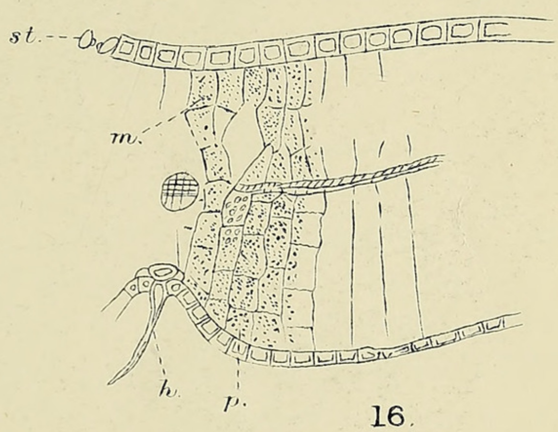

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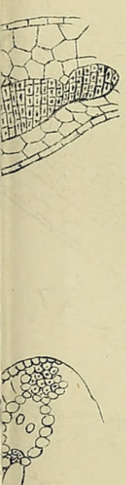

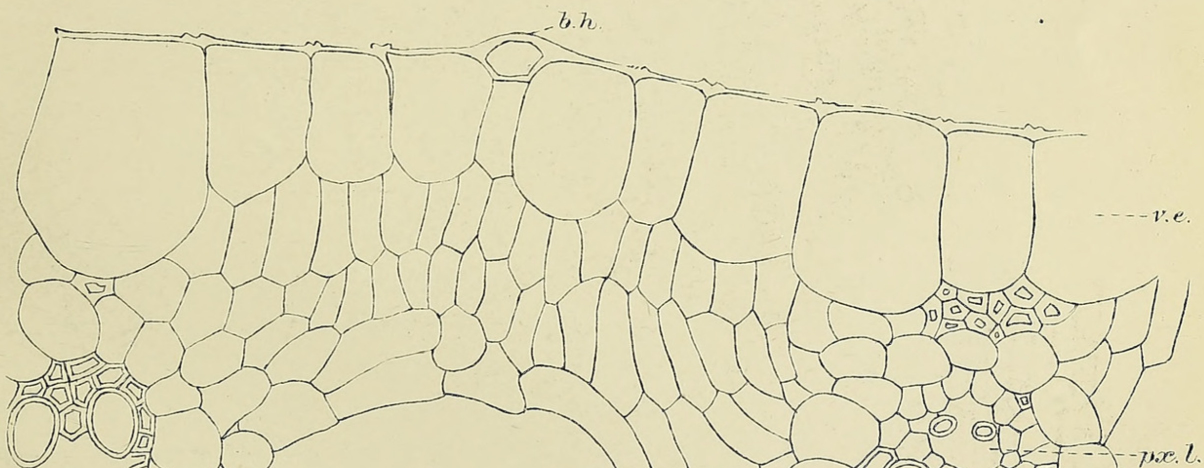

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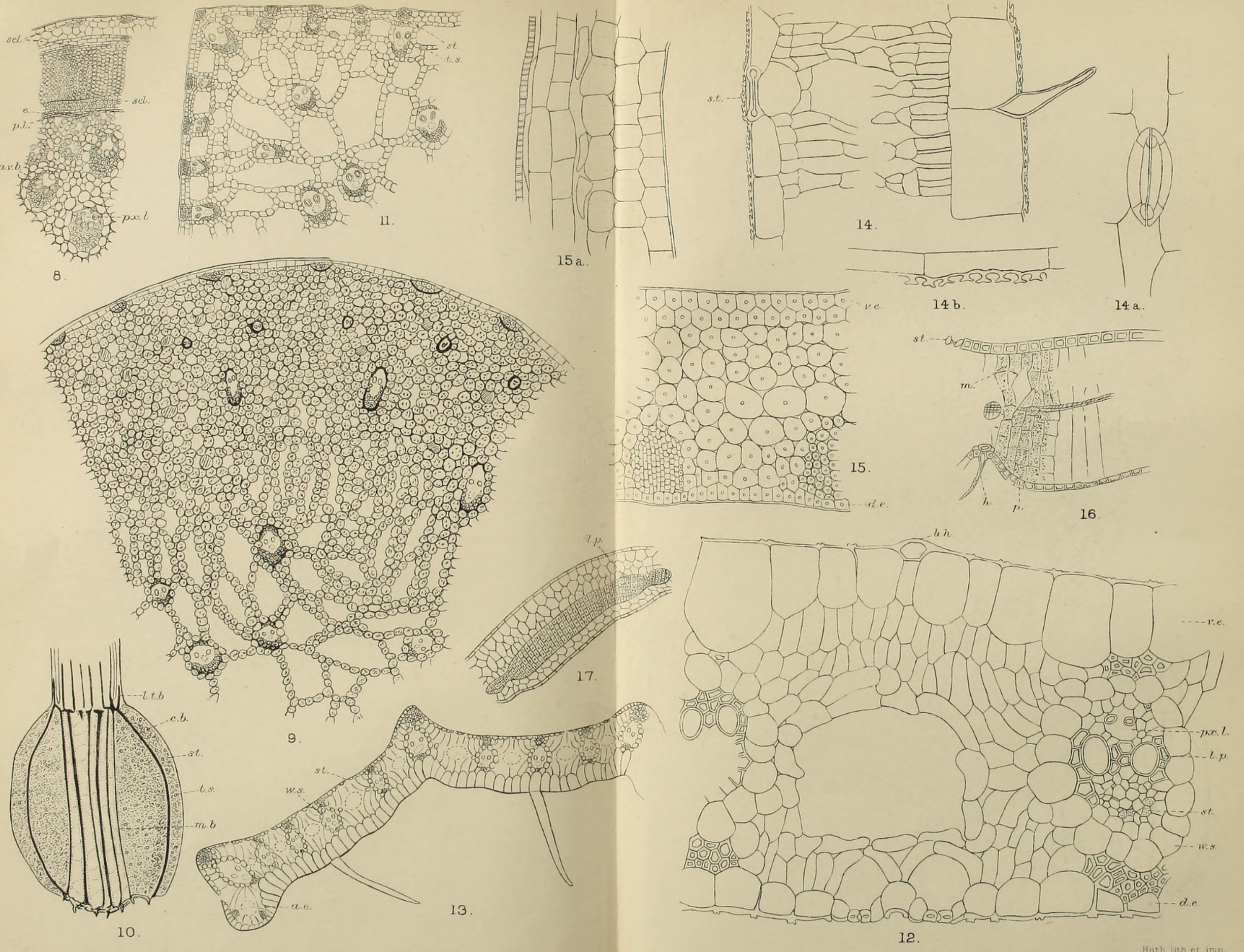

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