ON THE LEAF-TIP TENDRILS OF CERTAIN MONOCOTYLEDONS

BY

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1. Introduction

It has long been known that certain genera among the Liliaceae, and the one genus *Flagellaria* among the Farinosae, are distinguished by elongated leaf-tips which function as tendrils. Though I have been for some years engaged on a study of Monocotyledonous leaves, I have not found. in the literature of the subject, any connected account of the structure of these peculiar tendrils; it has therefore seemed to me worth while to attempt a comparative examination of them. In carrying out this study I have been obliged to rely chiefly upon herbarium specimens, since none of the species in question are native to Western Europe. For supplies of material I am indebted to the kindness of the Superintendent, Royal Botanic Garden, Sibpur, Calcutta; the Director, Royal Botanic Gardens, Kew; the Director and the Superintendent, the Botanic Garden, Cambridge; Miss G. Lister, and Professor A. C. Seward, F.R.S.

2. The Leaf-tip Tendrils of the Liliaceae

Leaves with tendril apices are characteristic of some or all the species in the case of five genera of the Liliaceae :—

Gloriosa				
Littonia	...	...	Melianthoideae	Uvularieae
Sandersonia				
Fritillaria	...	...	Liliaceae	Tulipeae
Polygonatum	...	...	Asparagoideae	Polygonateae

Gloriosa

The best-known of the Monocotyledonous genera with tendril leaf-tips is *Gloriosa*. Many authors have referred to these tendrils, but I have met with no description of their anatomy ; their physiology was studied by Darwin (7). I have been able to examine living plants of *Gloriosa superba*, L., a species which is cultivated in hot-houses in England. Here the earlier leaves, borne by the long climbing shoots, do not terminate in tendrils. They thus agree with the juvenile. leaves of the seedling, which, in those species about which we have records, are said to be non-tendrillar (7 and 8). Pl. II, Fig. 12 A, shows the second aerial leaf of a shoot of *G. superba* ; at the base it has a short closed sheath. The first aerial leaf of the same shoot was similar, but with a much longer closed sheathing base. According to Queva (9, p. 59) the first four leaves of the principal axis have closed sheaths. Higher on the shoot the mature type of leaf is borne ; it differs from those just described in the presence of a terminal tendril, and in the absence of a closed sheath at the base. Pl. II, Fig. 12 B, shows the end of a shoot with a number of leaves with apical tendrils, which curve downwards, so that the upper surface of the leaf forms the outer surface of the coils. When the tendril grasps a support, as in the lowest right hand leaf of this figure, it thickens considerably. Fig. 12 C shows a case in which the tendril tips of four leaves have become firmly interlocked. Pl. I, Fig. 1 represents the leaf of another species, *G. virescens*, Lindl., with its tendril tip. Though the particular leaf drawn was of a wider shape than those of G. *superba* shown in Pl. II. Fig. 12, the species is variable in this respect, and *G. virescens*, Lindl., var. *angustifolia* may even have linear leaves. *G. virescens* does not seem invariably to develop tendrils ; there is a flowering plant from Nyassa-Land in the Kew Herbarium, which shows no tendril formation.

The anatomical structure of the leaf-tip and tendril in *Gloriosa superba* are represented in Pl. 1, Figs. 2 and 3. Fig. 2 A indicates the structure of the leaf-tip just below the tendril ; the bundles are separate, and each has a patch of fibres above and below. In Fig. 2 B the tendril is thickening, and the amount of fibrosis has greatly increased, so that the bundles are all involved in one continuous sheath of fibres. Nearer the apex (Fig. 2 C) the tendril is still thicker—indeed it has become roughly circular in section—the bundles are reduced to three, presumably by the fusion of the laterals on either side, and the fibrous sheath has disappeared, except for patches in connexion with each of the three phloem groups. Higher still (Fig. 2 D) these three strands have fused into one vascular complex.

There seems to be a great deal of variation in the degree to which the tendrils thicken and become sclerised. Fig. 3 A is a transverse section (on a smaller scale) of a tendril which is more fibrous than that drawn in Fig. 2.

Fig. 3 B shows in greater detail the median bundle from another section of the same tendril, at a level where the fibrosis is less extreme. The xylem of the median bundle is narrowed and elongated—possibly owing to the pressure of the fibres in which it is embedded—so that, considered in three dimensions, it forms a thin ribbon in the median plane of the leaf.

Littonia

The genus *Littonia* is nearly related to *Gloriosa* ; I have not seen seedlings, but according to Queva (**9**, p. 139) the earliest leaves are non-tendrillar, as in *Gloriosa*. The tendril-tips of the mature leaves of both genera resemble one another in form and structure. Pl. I, Fig. 4 shows the leaf of *Littonia modesta*, Hook. and the changes in anatomy which take place in the passage from the tip of the limb to the tendril can be traced in Figs. 5 A—D. As in *Gloriosa*, the bundles are reduced to three in the tendril, and the partial fibrous sheaths are replaced by a single mass of fibres, in which the vascular strands are embedded. I was unable to obtain sections nearer to the apex of the tendril than that shown in Fig. 5 D, but there is little doubt that—as in *Gloriosa*—the three bundles fuse, for at the level of Fig. 5 D their xylems are separated by the width of one element only.

Sandersonia

The monotypic *Sandersonia aurantiaca*, Hook., of S. Africa, is a third plant nearly allied to *Gloriosa* and *Littonia*. Pl. II, Fig. 6 shows a tendrillar leaf of this species. Tendrils are apparently not always formed, for in most of the flowering specimens in the Kew Herbarium, the leaf apices, though long and slender, show no definite signs of coiling. The structure of the leaf-tip and tendril is illustrated in Figs. 7 A—C.

Fritillaria

The Uvularieae are the only tribe of the Liliaceae including more than one genus with leaf-tip tendrils, but the Tulipeae and the Polygonateae each contain one genus with the same peculiarity. Among the Tulipeae, certain species of *Fritillaria* have tendril leaves. Pl. II, Fig. 10 A shows a whorl of such leaves in the case of *F. verticillata*, Ledebour. This species is of particular interest, since some of the leaves show great reduction in connexion with tendril formation. Fig. 10 B. for instance, is from a shoot in which the lower leaves were linear, but the uppermost (those represented) were

so much narrowed as to be actually thread-like, so that the whole leaf may be said to be reduced to a tendril. Those *Fritillaria* tendrils of which I was able to cut sections, were markedly dorsiventral, and not fibrous (Fig. 11). As in the other Liliaceae, there was a three-stranded stage (Fig. 11 C); Fig. 11 D shows the apex of a tendril in which the vascular system consisted of one bundle.

Polygonatum

Pl. II, Fig. 8, shows the apex of a shoot of *Polygonatum sibiri-cum*, Delar., a plant which is known from Northern Asia and the Himalayan region. The coiled apical region of the tendril is flattened and ribbon-like; it was 1·5 mm. wide in the largest example I have seen. Pl. II, Figs. 9 A—E, show the anatomical structure of the tip of the limb and the tendril in this species. The bundles are reduced to three in Fig. 9 D and to one in the tip of the tendril, Fig. 9 E. A striking feature is the thick-walled epidermis on the lower side in the region of the midrib. The epidermis is two to three cells deep at the level of Figs. 9 B and 9 D; it is seen in greater detail in Fig. 9 C. This peculiarity is gradually lost, however, towards the apex, and in Fig. 9 E the lower epidermis in the midrib region consists of only a single layer of large cells.

So far as I have been able to observe, the tendril of *Polygonatum* differs from that of *Gloriosa*, *Littonia* and *Sandersonia*, and resembles that of *Fritillaria*, in not becoming fibrous. But in the thickest tendril I was able to examine, the xylem of the median bundle was somewhat more developed than in the example figured here.

3. The Leaf Structure of the Flagellariaceae

In the case of the Liliaceae we find five genera with leaftip tendrils, distributed among three of the tribes of a very large Family, including nearly 200 genera. The only other genus among Monocotyledons which possesses tendril leaf-tips—*Flagellaria*—occupies however a very different position systematically, since it is one of the three genera which make up the small Family, Flagellariaceae, belonging to the Farinosae. In a recent paper (6) I have given a sketch of the leaf structure of this Cohort, omitting, however, this particular Family, because it seemed better to consider it in connexion with the leaf tendrils with which we are here concerned. Since the leaf anatomy of the Flagellariaceae appears to have remained hitherto undescribed, I propose here to say something about all the three genera, though *Flagellaria*, which gives its name to the Family, is the only one which possesses tendrils.

Flagellaria

The leaf of *Flagellaria indica*, L., is shown in Plate III, Fig. 13. It has a conspicuous sheath (*sh*) sharply separated from a well-marked limb (*l*) terminating in a tendril (*t.*) For comparision I have drawn a seedling (Fig. 14), in which it will be seen that scale leaves with no differentiated blade (*sc.*) are succeeded by juvenile foliage leaves (such as *l.*) which have expanded limbs, but in which the apical tendril is absent, its place being taken by an acuminate tip. The leaf-sheath is longer in proportion to the limb in the juvenile leaves than in the mature leaves. I do not know how soon tendrils make their appearance; they were still absent in the oldest seedlings I have been able to obtain, which bore ten leaves, and Darwin records that a young plant under his observation, which was 12 inches in height and bore 15 leaves, had not a single leaf produced into a tendril (7). The tendril, which coils forwards towards the ventral surface of the leaf, tends rather to a flat ribbon-like form. The anatomy of the leaf-tip and tendril is illustrated in Figs. 15 A—C. Fig. 15 A shows the structure of the leaf-tip just below the tendril. The median bundle (*m. b.*), the main laterals (*m. l.*) and the minor bundles, have each an individual fibrous sheath. Fig. 15 B is a section of a somewhat thickened tendril, in which the mesophyll, forming the main part of the section, is thick-walled but not sclerised. The bundles, which lie in one horizontal plane towards the dorsal surface of the tendril, are enclosed in a common sheath of fibres, which are more densely sclerised and thicker-walled on the side towards the phloem. Fig. 15 C shows the structure of the thickest coiled part of another tendril. The bundles, as in the previous case, have a common fibrous sheath, while the mesophyll has also become sclerised in the region indicated by cross-hatching.

Susum

This genus is characterised by large simple leaves, which are said sometimes to exceed six feet in length. I have not been able to examine them as thoroughly as I should wish, but I have had the opportunity of cutting sections of one leaf of *S. anthelminthicum.* Blume, whose lanceolate limb was markedly asymmetrical about the midrib. The structure of the leaf-sheath is shown diagrammatically in Plate III, Figs. 16 *A* and *B*. In the thicker parts of the leaf-base there are several series of bundles, each bundle being enclosed in a massive coat of fibres. There is a series of small strands close to the upper, and another close to the lower surface; in the members of both these series the vascular tissue occupies only a

minute proportion of the bundle area—the remaining space being filled by a mass of fibres. These bundles may be compared with some of those, for instance, in the leaf of *Agave*, and may be considered as having entered on the down-grade path which leads from a true vascular bundle to a mere strand of fibres (1, pages 493-4). These small superficial bundles of the *Susum* sheath have also another interesting peculiarity—namely that the members of the series towards the upper surface (*i.b.* 2) are seen to be inversely orientated in all those cases in which the vascular tissue is well enough developed to be distinguishable. There are also some larger bundles (*i.b.* 1), not belonging to the upper inverted series, but agreeing with it in having their xylems directed downwards and phloems upwards. In the marginal region of the sheath (Fig. 16 B) the inverted bundles die out; in this figure only one is visible. Inversely orientated strands can be followed up into the midrib region of the limb.

Joinvillea

The leaf of *Joinvillea elegans* Gaudich., differs greatly from that of *Flagellaria* or of *Susum*. The following description of the anatomy is based upon the study of a single dried leaf. The top of the sheath (*sh.*) and the base of the "plicate" limb (*l.*) are represented in Plate III, Fig. 17. There is a conspicuous ligule (*lig.*) at the junction of the two. Fig. 18 A shows the structure of the leaf sheath; as in *Susum*, there is more than one series of bundles; each strand is enclosed in a fibrous coat, and some of the strands even consist exclusively of fibres. The hypodermal region below the ventral surface of the sheath is conspicuously meristematic, the cells being arranged in radial rows; Fig. 18 B shows these parallel files on a larger scale. Meristematic activity in this region is not uncommon in Monocotyledonous leaf-sheaths. As indicated by Figs. 18 C and D, the plication of the limb originates by invaginations which penetrate from the dorsal surface between the main bundles, while invaginations belonging to an alternating series pass in from the ventral surface. The bases of these longitudinal grooves are occupied by enlarged epidermal cells, marked with a cross in Figs. 18 C and D. These cells are a striking feature of sections of this leaf, since they, and the smaller hypodermal cells beneath them, remain clear and colourless when the preparations are stained with methyl green; they are shown on a larger scale in Fig. 18 E. It will be noted in Fig. 18 D, drawn from a section of the limb not far from the apex, that the bundles have come to lie slightly laterally to the ridges and furrows, and thus not immediately above and below the enlarged cells. I have

already described the occurrence of similar hypertrophied epidermal cells lining the bases of invaginations in the leaf of *Curculigo recurvata*, Dryand. (5, Fig. 17, p. 341); but there are differences in detail, since in *Curculigo* the hypoderm is not involved and the passage between the enlarged and normal epidermal cells is more gradual. But in both cases these enlarged epidermal cells are associated with the development of a plicate leaf; they appear to correspond to the "motor cells" which are concerned in the rolling and folding of Grass leaves, but differ from them in being developed on both surfaces of the leaf, instead of only on the upper surface. As I have not seen the leaf of *Joinvillea* in the living state, I cannot say whether these cells have the power of opening and closing the fan-like folds of the limb, as one might expect by analogy with the action of the motor cells of Grasses.

In previous papers I have described the origin of "plication" by invagination in the Palms (4), Cyclanthaceae, Liliaceae and Amaryllidaceae (5), and Iridaceae (3). The case of *Joinvillea* furnishes a comparable example from the Farinosae—a Cohort in which this mode of development has not been hitherto observed.

4. Comparison and Conclusions

In general appearance, the leaf-tip tendrils of all those Monocotyledons which we have been considering conform to one simple type. Their morphological interpretation is not, however, correspondingly easy, and it is possible that the same explanation will not apply to all. The leaf of *Flagellaria* is more completely differentiated than that of the tendril-bearing Liliaceae. On the phyllode theory (1) I should interpret the leaf of *Flagellaria* as consisting of a sheath succeeded by a limb which is a horizontally expanded petiole, and I should thus look upon the tendril as representing the apical part of this flattened petiole. In the case of the Liliaceous genera, it may be that the morphology is, in reality, the same, and that the limb is of petiolar nature, while the leaf-sheath—in the mature tendril-bearing leaves—is reduced almost to nothing. On the other hand the limb in these species may possibly be of leaf-sheath nature, in which case the tendril may represent either the apex of the leaf sheath, or the vestigial rudiment of a petiole. The difficulty in elucidating these tendril leaves is the greater, because there are no cases, among the Dicotyledons, of simple leaves with tendril apices, with which the Monocotyledonous cases could be compared; and in the only other tendril-bearing Monocotyledon—*Smilax*—these organs are so extremely remote in morphology and structure from the leaf-tip tendrils here described, that they are useless for purposes of comparison (2).

When we come to compare among themselves the leaf-tip tendrils which we have described in this paper, we find that they present a certain general similarity, but also a number of out-standing differen-ces. Externally the most noticeable divergence relates to the direction of coiling. Whereas in all the five Liliaceous genera the tendrils coil downward (*i. e.* the upper or ventral leaf surface forms the outer surface of the coils) in the case of *Flagellaria* the curvature is in the opposite direction—the tip curling inwards. In anatomy also—as has been shown in the descriptive section of this paper—*Flagellaria* is sharply marked off from the Liliaceous cases. If Plate III, Fig. 15 C, which represents a section of the thickened tendril of *Flagellaria*, be compared with Plate I, Fig. 3 A, in which the corresponding region of *Gloriosa* is shown, it will be seen that the type of structure is essentially different. In *Flagellaria* there is a series of bundles, recalling the arrangement met with in the leaf of *Restio*, another member of the Farinosae (6. Plate I, Fig. 1), while in the corresponding region of the Liliaceous genera, the strands are reduced to three ; in *Flagellaria*, again, the main mass of the sclerotic tissue is independent of the vascular strands, instead of being closely associated with them as in *Gloriosa*. In *Gloriosa* indeed, one cannot, in the thickened tendril, discriminate between bundle-sheath fibres and fibrous cortex, but in *Flagellaria* these two regions are separate and readily distinguishable.

When we leave *Flagellaria* on one side and compare the Liliace-ous genera among themselves, we find that, though the tendril anatomy of the Uvularieae—*Gloriosa* (Plate I, Fig. 3 A), *Littonia* (Plate I, Fig. 5 C.) and *Sandersonia* (Plate II, Fig. 7 C)—conforms with minor divergences to one general plan, yet this general plan is somewhat different from that of *Polygonatum* (Polygonateae) on the one hand (Plate II, Fig. 9 D), or *Fritillaria* (Tulipeae) on the other (Plate II, Fig. 11 C).

The fact that in the six Monocotyledonous genera which have leaf-tip tendrils, these organs vary among themselves, anatomically, in the way which we have indicated, is, I think, of some significance. On the theory that structure is determined by function, one might have expected to find that these leaf-tip tendrils would conform to one anatomical type, whether the plants bearing them were closely related or not. But what we actually find is that they are by no means uniform, but show among themselves just those degrees of resemblance and difference which might have been anticipated if the anatomical ground-plan of any organ be supposed to depend, not on the function it is destined to perform, but on the position, in the Natural System

of the species to which it belongs. In other words, the study of the leaf-tip tendrils of Monocotyledons leads us to the view that the general anatomical scheme on which these organs are constructed is determined by the inherent anatomical tendencies of the species, rather than by the response to a common physiological need.

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Explanation of the Plates
PLATE I

[Throughout the plates the following notation is used :—$xy.$, xylem (black) : $ph.$, phloem, (white) ; $f.$, fibres (dotted) ; $u. e.$, upper epidermis ; $l. e.$, lower epidermis.]

Fig. 1.—*Gloriosa virescens*, Lindl., leaf from the Sudan, Kew Herbarium, ($\times$ $\frac{2}{3}$).

Figs. 2 and 3.—*Gloriosa superba*, L.

Fig. 2 A—D, series of sections through leaf apex and tendril from below upwards ($\times$ 21).

Figs. 3 A and B, thickened region of another tendril; Fig. 3 A, transverse section of tendril ($\times$ 10); Fig 3 B, median bundle from a transverse section of the same tendril, at a level where there is slightly less fibrosis than in Fig. 3 A ($\times$ 141): *ph. f.*, fibres outside phloem.

Fig. 4.—*Littonia modesta*, Hook., leaf ($\times$ $\frac{2}{3}$).

Fig. 5 A—D.—*Littonia Keiti*, Leicht. (*L. modesta*, Hook.), specimen from Temberland, Kew Herbarium, series of transverse sections upwards from below through one leaf apex and tendril ($\times$ 21).

PLATE II

Figs. 6 and 7.—*Sanderonia aurantiaca*, Hook.

Fig. 6, leaf of specimen from Swaziland, Kew Herbarium, ($\times$ $\frac{2}{3}$)

Fig. 7 A, specimen from Natal, transverse section near leaf apex ($\times$ 10).

Figs. 7 B and C, specimen from Swaziland, transverse sections nearer apex of leaf than Fig. 7 A ($\times$ 34).

Figs. 8 and 9.—*Polygonatum ibiricum*, Delar.

Fig. 8. apex of shoot with young leaves, Kew Herbarium, ($\times$ $\frac{2}{3}$)

Figs. 9 A, B, D, E, series of transverse sections of apical region of leaf, from below upwards, including tendril ($\times$ 10). Fig, 9 C, median bundle of Fig. 9 B on a larger scale ($\times$ 34); *d. e.*, thick-walled dorsal epidermis.

Figs. 10 and 11.—*Fritillaria verticillata*, Ledebour.

Fig. 10 A, a node with four leaves, slightly reconstructed, since the herbarium material used was imperfect ($\times$ $\frac{2}{3}$).

Figs. 10 B and C, examples of very narrow leaves from the Cambridge Botany School Herbarium ($\times$ $\frac{2}{3}$).

Figs. 11 A and D, transverse sections through one tendril ($\times$ 21).

Fig. 11 B, median bundle of Fig. 11 A ($\times$ 86).

Fig. 11 C, transverse section through another tendril ($\times$ 10).

Fig. 12, *Gloriosa superba*, L. (garden variety).

Fig. 12 A, second aerial leaf of shoot ($\times$ $\frac{2}{3}$).

Fig. 12 B, shoot apex ($\times$ $\frac{2}{3}$).

Fig. 12 C, tips of four leaves with tendrils interlocked ($\times$ $\frac{2}{3}$).
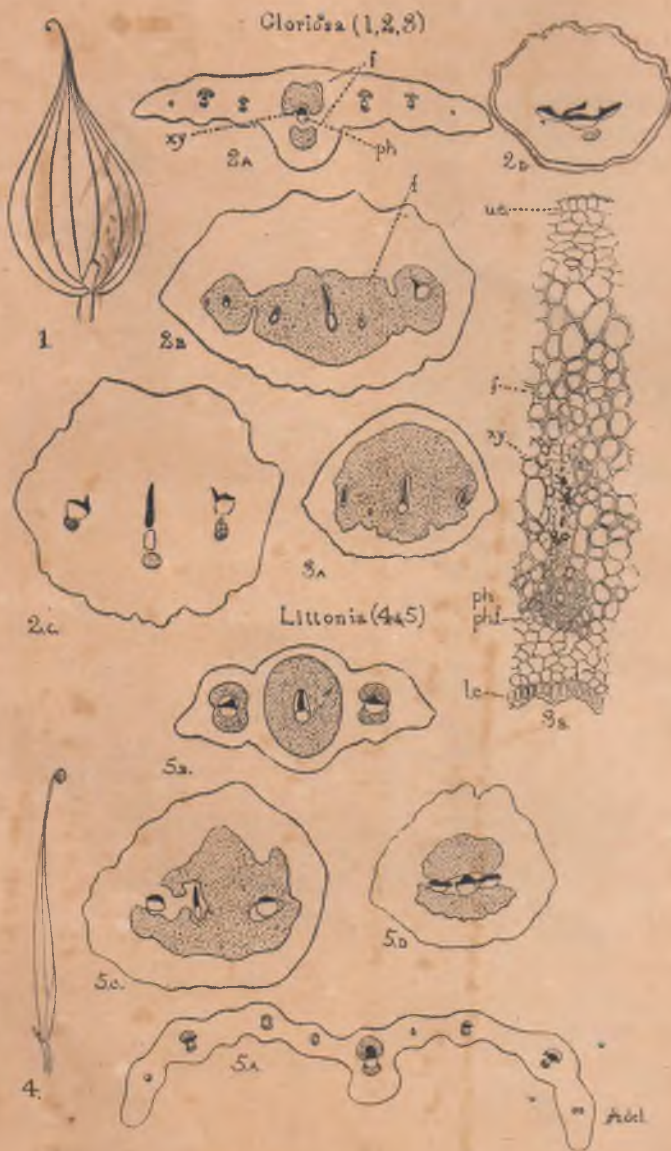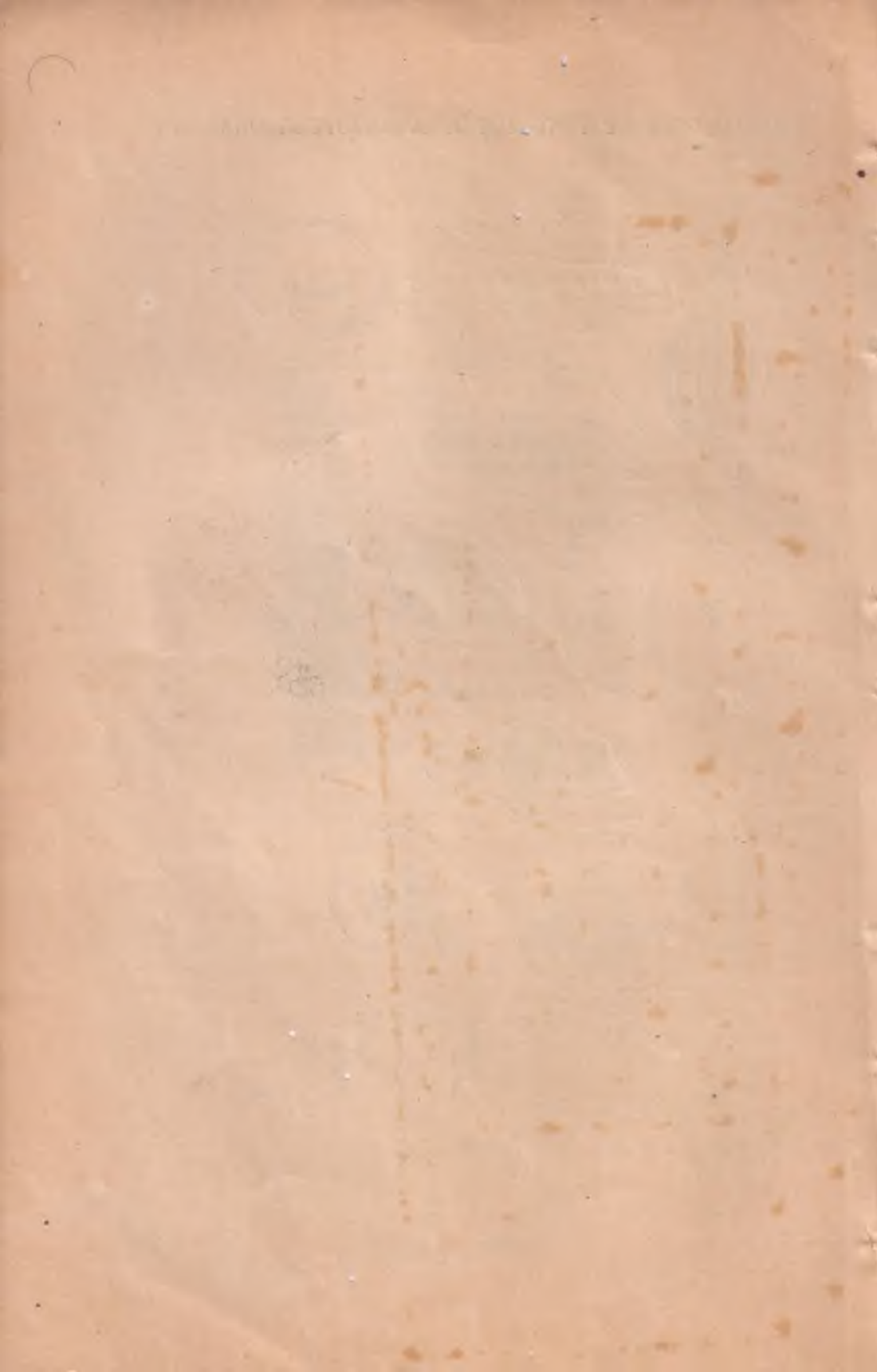
PLATE I.

PLATE II

FLAGELLARIACEÆ

Flagellaria (13,14,15)

Susum (16)

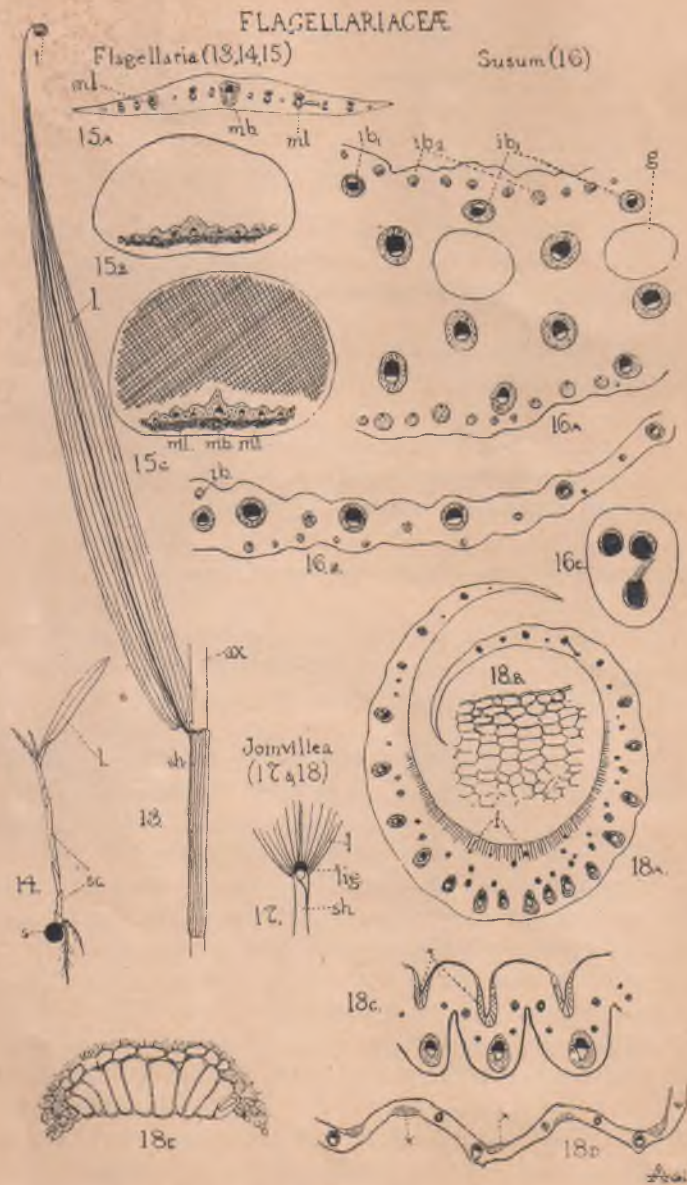Jomvillea (17 & 18)
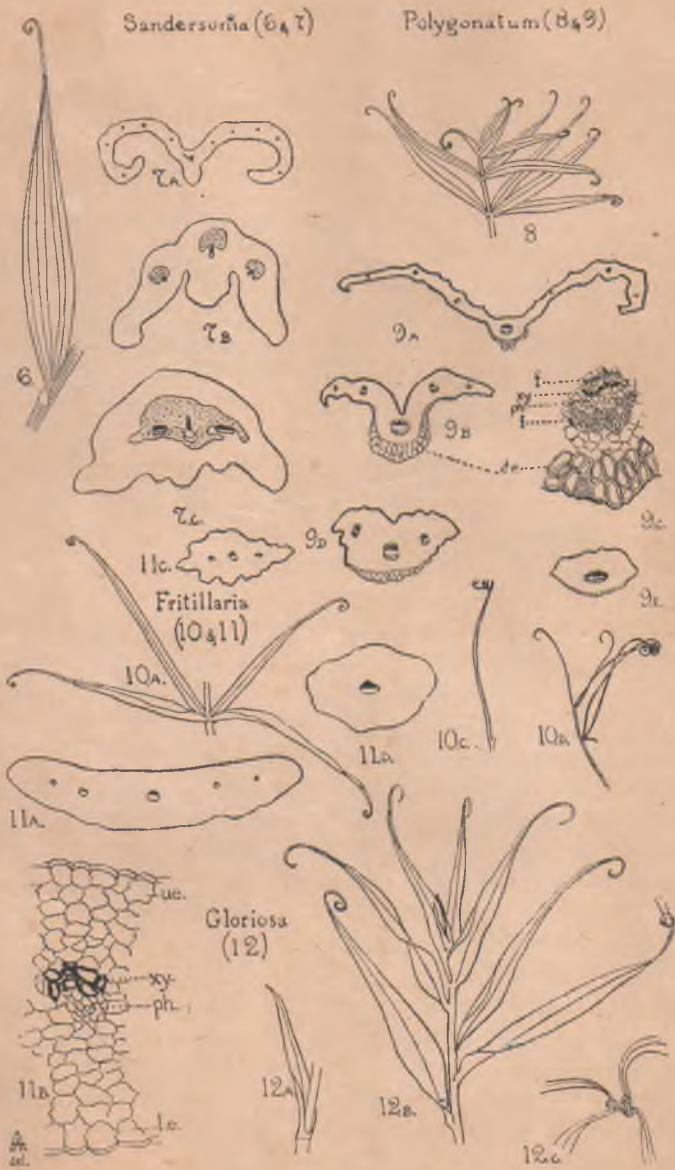
PLATE III

PLATE III

Flagellariaceae

Figs. 13, 14, 15.—*Flagellaria indica*. L.

Fig. 13, mature leaf ($\times \frac{2}{9}$); *ax.*, axis; *sh.*, sheath: *l.*, limb; *t.*, tendril.

Fig. 14, seedling with seed (*s.*); scale leaves (*sc.*); and foliage leaves (*l*).

Fig. 15 A, transverse section of a leaf near apex just below tendril; *m. b.*, median bundle; *m. l.*, main laterals ($\times$ 10).

Fig. 15 B, transverse section of a somewhat thickened tendril ($\times$ 10).

Fig. 15 C, transverse section of a tendril which had coiled and thickened; the cross-hatching indicates mesophyll cells which have become fibrous ($\times$ 10).

Fig. 16.—*Susum anthelminthicum*, Blume.

Fig. 16 A, transverse section of a small part of sheath region of leaf ($\times$ 10); *i. b.* $_1$ and *i. b.* $_2$ inversely orientated vascular bundles, *g.*, ? gum spaces.

Fig 16 B, transverse section of small part near margin of sheath region of leaf ($\times$ 10).

Fig 16 C, transverse section near tip of leaf borne on the inflorescence axis of *Susum* ? *anthelminthicum* ($\times$ 10). At this level the chief part of the bundle is formed by xylem; at a higher level the three bundles fuse.

Figs. 17 and 18.—*Joinvillea elegans*. Gaudich.

Fig. 17, base of leaf-limb ($\times \frac{2}{9}$); *sh.*, sheath; *lig.*, ligule: (indicated in black); *l*, plicate limb.

Fig. 18 A, transverse section of sheath, hairs omitted ($\times$ 6); *f.*, groups of fibres; the lines at right angles to the upper epidermis indicate the radial files of elements, due to meristematic activity.

Fig. 18 B, part of transverse section towards ventral surface more enlarged to show radial files of cells below upper epidermis ($\times$ 34).

Fig. 18 C, part of transverse section of lower part of limb, to show origin of plication by invagination, hairs omitted; the lower epidermis has enlarged cells (marked with a cross) at the base of the invaginations ($\times$ 10).

Fig. 18 D, part of transverse section of limb, not far from apex; hairs omitted; groups of enlarged cells in both upper and lower epidermis.

Fig. 18 E, group of enlarged cells from lower epidermis, similar to left hand group marked with a cross in Fig. 18 D, more highly magnified ($\times$ 86).