



## I. INTRODUCTION.

IN the course of the last four years I have discussed, in a sequence of papers in this and other journals,<sup>1</sup> the interpretation of the Monocotyledonous leaf in terms of the phyllode theory. In certain cases this interpretation presents little difficulty. There is nothing strained, for instance, in the view that such a leaf as that of *Triglochin maritimum* is a petiolar phyllode; its sheathing base is separated by a ligule from a limb, which is more or less cylindrical in form with a slightly flattened ventral surface—both in its appearance and in its 'radial' anatomy, this limb is distinctly petiolar. But the extension of the phyllode theory to those Monocotyledons which have a leaf-blade showing a general resemblance to the lamina of a Dicotyledon is attended with more difficulty. To many minds there seems, *a priori*, to be an element of improbability in the view, first suggested by Henslow,<sup>2</sup> that these blades are not true laminae, but are elaborations of the distal region of the petiole. In previous communications I have considered the nature of the leaf-blade in certain special cases, but I propose now to take a wider survey, and to submit the subject to a more rigorous analysis, paying special attention to the comparison between the ontogeny of Monocotyledonous and Dicotyledonous leaf-blades. The observations in the present paper relate to the 'lamina' as it appears in the leaves of examples from among the Helobieae, Principes, Synanthae, Spathiflorae, and Liliiflorae, and also of certain Dicotyledons selected for study because of their apparent resemblance to some of the Monocotyledons in question. In the case of the Glumiflorae I am contenting myself with a passing reference, since I hope to discuss the leaves of the Gramineae and Cyperaceae in a later paper.

I am indebted for material to the Director of the Royal Botanic Gardens, Kew; to the Director and to the Superintendent of the Cambridge Botanic Garden; to Dr. H. E. Durham and to Mr. J. H. Maiden, F.R.S., of Sidney. Two of the illustrations in the present paper are drawn from preparations made by the late Miss Ethel Sargent.

## II. OBSERVATIONS ON THE ORIGIN OF THE 'LAMINA' IN THE LEAF OF CERTAIN MONOCOTYLEDONS.

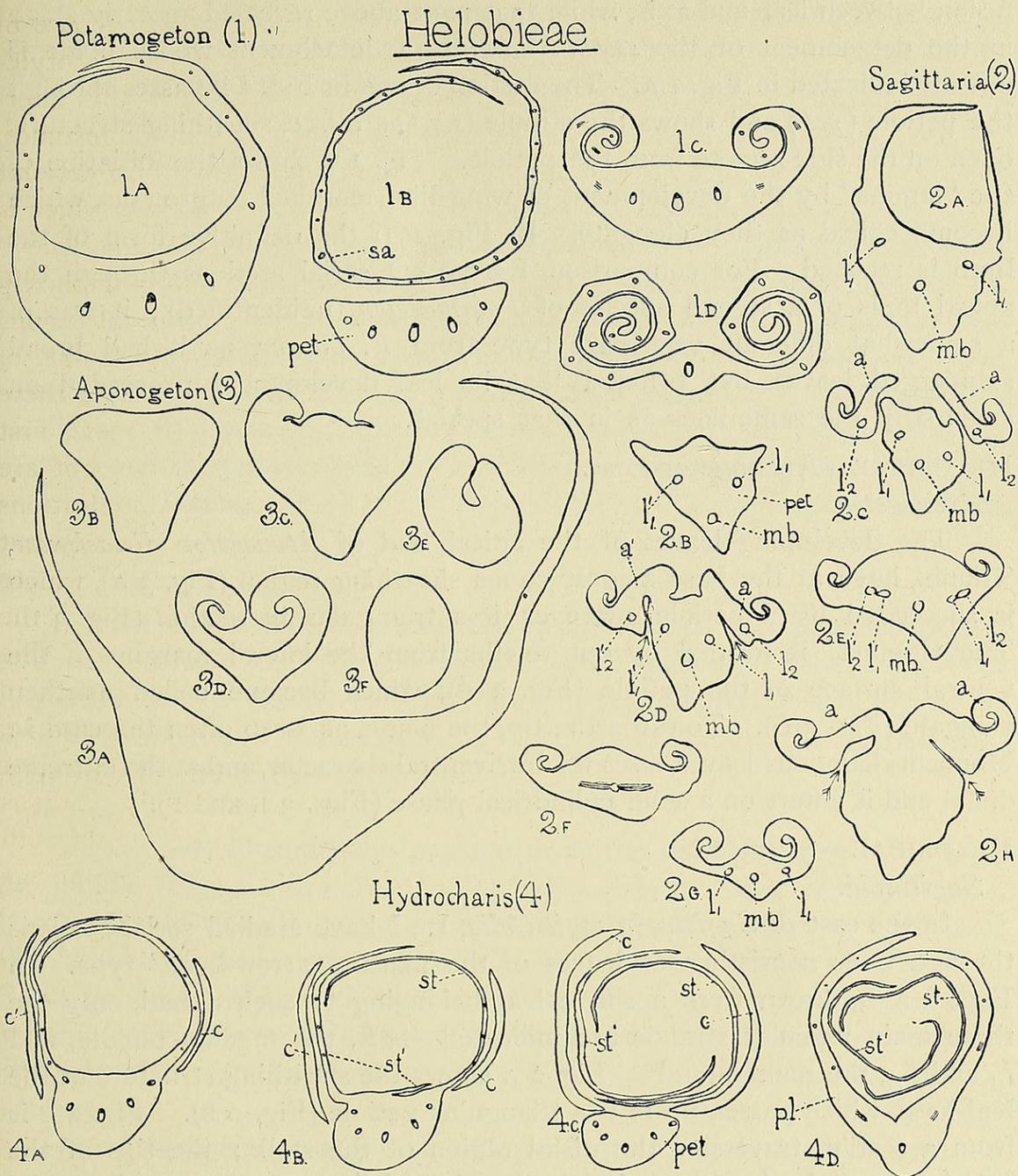
## HELOBIEAE—Potamogetonaceae.

*Potamogeton*.

Sections of the apical buds of shoots of *Potamogeton natans*, L., bearing leaves of the floating type, show that these leaves in their young stages have at their base an extremely short sheathing region. In the case of the leaf illustrated in Figs. 1 A–D, the section represented in Fig. 1 A was the only one, in a series cut to a thickness of  $14\mu$ , which could accurately be

<sup>1</sup> Arber, A : (1918), (1919<sup>1</sup>), (1920<sup>1</sup>), (1920<sup>2</sup>), (1920<sup>3</sup>), (1921<sup>1</sup>), (1921<sup>2</sup>), (1921<sup>3</sup>), (1922<sup>1</sup>), (1922<sup>2</sup>).

<sup>2</sup> See reference in Arber, A. (1918), p. 470.



FIGS. 1-4. Figs. 1 A-D, *Potamogeton natans*, L., series of transverse sections from below upwards through a young leaf, from sheath, Fig. 1 A, to 'lamina', Fig. 1 D ( $\times 47$ ); *pet.*, petiole; *s.a.*, stipula adnata. Fig. 2, *Sagittaria sagittifolia*, L., Figs. 2 A-G, serial sections through one young leaf ( $\times 23$ ) from sheath, Fig. 2 A, to 'lamina', Fig. 2 G; *a.* and *a'*, auricles; *pet.*, petiole; *m.b.*, median bundle; *l.*<sub>1</sub> and *l'*<sub>1</sub>, main lateral bundles; *l.*<sub>2</sub> and *l'*<sub>2</sub>, bundles given off from *l.*<sub>1</sub> and *l'*<sub>1</sub> to supply auricles; Fig. 2 H, transverse section of another young leaf ( $\times 23$ ) at level of detachment of auricles, vascular bundles omitted. In Figs. 2 D and 2 H the arrows indicate the invaginations which detach the auricles. Figs. 3 A-F, *Aponogeton distachyum*, Thunb., series of transverse sections through one leaf from below upwards ( $\times 47$ ), vascular bundles omitted. Fig. 4 A-D, *Hydrocharis Morsus-ranae*, L., series of transverse sections through one leaf passing from sheath, Fig. 4 A, to 'lamina', *pl.*, Fig. 4 D; *pet.*, petiole; *st.* and *st'*, stipules; *c.* and *c'*, basal cordate lobes of 'lamina' ( $\times 23$ ).

described as passing through the leaf-sheath; the section next below showed fusion between leaf and axis, while that next above revealed an early stage in the detachment of the *stipula adnata*—a detachment whose plane is already indicated in Fig. 1 A. The section drawn in Fig. 1 B passes through the petiole (*pet.*) and shows the stipule (*s.a.*) as a free, sheathing structure, open on the side remote from the petiole. Fig. 1 C shows the initiation of the 'lamina' by the development of wing-like marginal outgrowths, which become coiled as they elongate. In Fig. 1 D the definitive form of the limb is reached. For comparison, I have cut serial sections through the apical buds of a second species of *Potamogeton* (unidentified); it was of a somewhat different vegetative type from *P. natans*, as it had broad submerged leaves, but I found that its leaf development proceeded on essentially the same lines as in that species.

#### HELOBIEAE—Aponogetonaceae.

##### *Aponogeton.*

The developing leaves of the apical bud of *Aponogeton distachyum*, Thunb., have at the base a conspicuous sheathing region (Fig. 3 A), which is succeeded by a petiole, more or less triangular in section (Fig. 3 B). The 'lamina' is formed by outgrowths from the lateral margins of the ventral surface of the petiole (Fig. 3 C), which become coiled as they elongate (Fig. 3 D). Towards the tip, the blade, as is so often the case in Monocotyledonous leaves, loses its dorsiventral character, and at the extreme distal end it enters on a solid cylindrical phase (Figs. 3 E and F).<sup>1</sup>

#### HELOBIEAE—Alismaceae.

##### *Sagittaria.*

In the case of *Sagittaria sagittifolia*, L., I have studied serial sections through buds consisting of leaves of the mature 'arrow-head' type. In Figs. 2 A-G, drawn from a single leaf belonging to such a bud, only the three main vascular strands are indicated—*m.b.*, the median bundle, and *l.*<sub>1</sub> and *l.*'<sub>1</sub>, the main laterals. Fig. 2 A shows the sheathing structure at the leaf-base, which passes up into a triangular petiole (Fig. 2 B). Fig. 2 C is from a section traversing the distal region of the stalk; the tips of the auricles (*a.* and *a.*') with their bundles (*l.*<sub>2</sub> and *l.*'<sub>2</sub>) are cut on either side. Fig. 2 D shows the connexion of the auricles with the petiole. In Fig. 2 E the origin of the vascular supply of the auricles can be traced; the lateral bundles (*l.*<sub>1</sub> and *l.*'<sub>1</sub>) bifurcate—the outer half in each case being destined to pass down into an auricle. This section also indicates how the main part of the 'blade' comes into existence by the development of lateral wings from the petiole. At a slightly higher level there is a fusion between the median bundle and the laterals (Fig. 2 F); the general arrangement of the developing veins is perhaps not inconsistent with the morphological

<sup>1</sup> Arber, A. (1922<sup>2</sup>).

interpretation of the arrow-head 'lamina' which I have suggested in a former paper.<sup>1</sup> In Fig. 2 G the upper part of the leaf-limb is reached. Fig. 2 D shows the detachment of the auricles by means of invaginations, indicated by arrows, and the same stage is also seen in Fig. 2 H, drawn from another leaf.

#### HELOBIEAE—Hydrocharitaceae.

##### *Hydrocharis*.

Microtome sections through the leaf-buds of *Hydrocharis Morsusranae*, L., show that the orbicular floating leaves are sheathing at the base (Fig. 4 A). The cordate basal lobes of the 'lamina' are cut through on either side and hence appear as detached objects (*c.* and *c'*). The sheath passes upwards into the paired stipules (*st.* and *st'*), which are seen in Fig. 4 B in process of separation from the petiole. In Fig. 4 C the two stipules and the petiole (*pet.*) are entirely free from one another. Fig. 4 D shows the 'lamina' (*p.l.*), which is produced by lateral expansion of the petiole.

#### PRINCIPES—Palmae.

I have considered the Palm-leaf in some detail in a previous paper,<sup>2</sup> and have shown that in this family the apparently plicate leaf-limb originates, not by folding—as has been generally supposed—but by means of a series of invaginations involving the petiolar tissues. So I shall now refer very briefly to two cases only.

##### *Areca*.

Figs. 5 A–E illustrate the passage from the sheath (Fig. 5 A) through the petiole (Fig. 5 B) to the 'lamina' (Fig. 5 E) in *Areca sapida*, Soland. It will be seen that the plication arises by means of a series of dorsal and ventral invaginations penetrating between the main vascular strands (*m.b.*, *l.*<sub>1</sub>, *l.*<sub>2</sub>, *l.*<sub>3</sub>, *l'*<sub>1</sub>, *l'*<sub>2</sub>, *l'*<sub>3</sub>), which can be followed from section to section. The process is a rapid one; a distance of only 0.35 mm. intervenes between the first sign of the first invagination and the stage represented in Fig. 5 D.

##### *Oreodoxa*.

I add three drawings (Figs. 6 A–C) to illustrate the relations, in form and skeletal system, between the petiole and 'lamina' in a second case—*Oreodoxa regia*, H. B. et K. The bundles are lettered as in Fig. 5. The first pair of invaginations, indicated by arrows, come into view in Fig. 6 B.

#### SYNANTHAE—Cyclanthaceae.

##### *Carludovica*.

Many years ago Eichler,<sup>3</sup> in his memoir on the developmental history of Palm-leaves, drew attention to their resemblance to those of the Cyclanthaceae—a comparison which has frequently been emphasized by

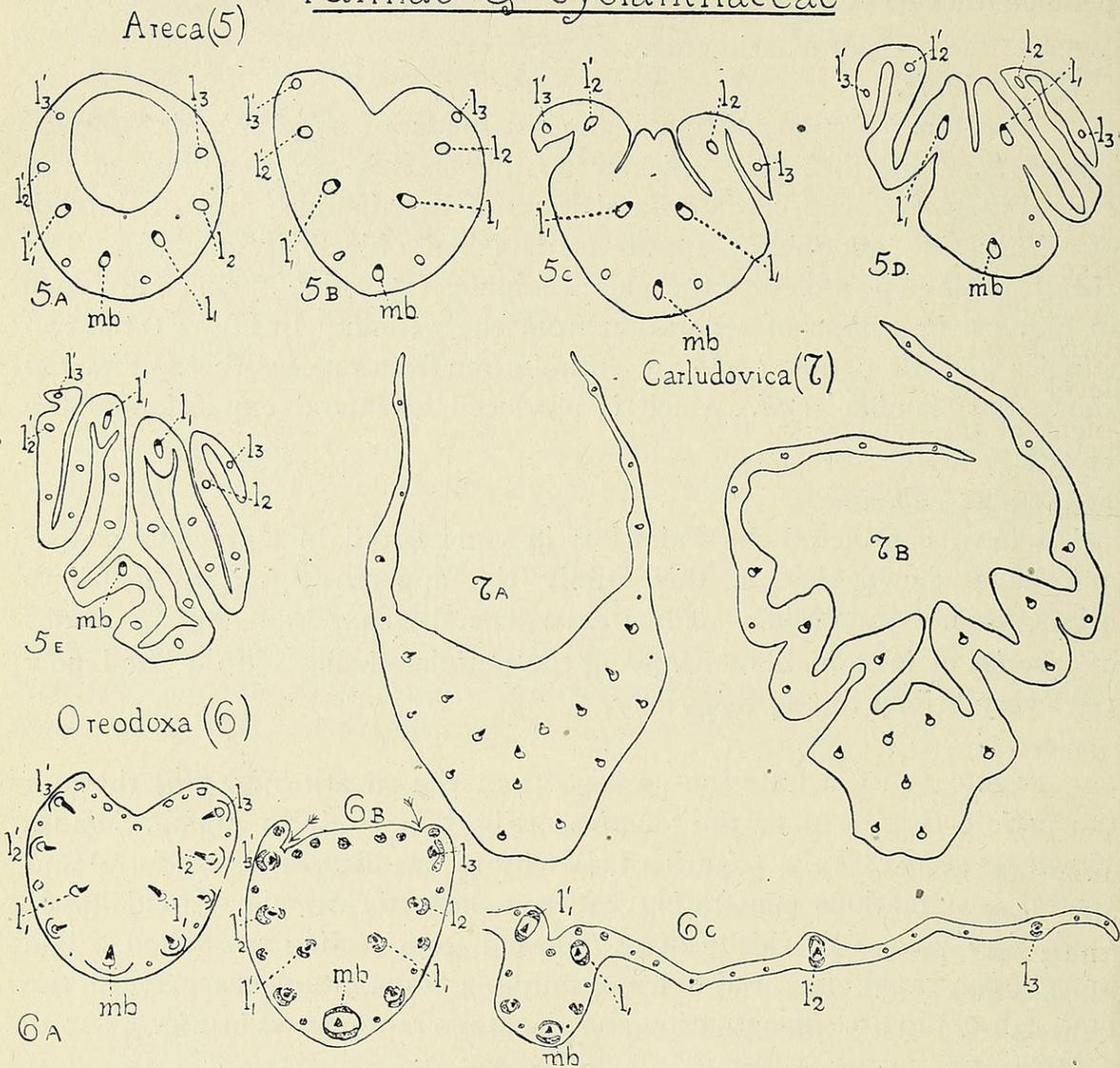
<sup>1</sup> Arber, A. (1921<sup>2</sup>).

<sup>2</sup> Arber, A. (1922<sup>1</sup>).

<sup>3</sup> Eichler, A. W. (1885).

more recent writers.<sup>1</sup> Eichler interprets the leaves of the Cyclanthaceae as owing their form to folding, the agency to which he also attributes the plicated appearance of the Palm-leaf. I have found, however, on studying

### Palmae & Cyclanthaceae



FIGS. 5-7. Figs. 5 A-E, *Areca sapida*, Soland., series of transverse sections ( $\times 47$ ) through one leaf, from sheath, Fig. 5 A, to plicate 'lamina', Fig. 5 E; *m.b.*, median bundle; *l*<sub>1</sub>, *l*<sub>2</sub>, *l*<sub>3</sub>, *l*'<sub>1</sub>, *l*'<sub>2</sub>, *l*'<sub>3</sub>, principal lateral bundles. In Figs. 5 C-E the invaginations are shown which penetrate between the bundles of the petiole, Fig. 5 B. Figs. 6 A-E, *Oreodoxa regia*, H. B. et K., sections from a series through the first foliage leaf (third plumular leaf) of a seedling ( $\times 14$ ). Lettering of bundles as in Fig. 5; Fig. 6 A, petiole; Fig. 6 B, first signs of invaginations indicated by arrows; Fig. 6 C, half the 'lamina', showing eventual distribution of bundles. Figs. 7 A, B, *Carludovica Plumerii*, Kunth, transverse sections of young leaf passing through sheath, Fig. 7 A, and regions where invagination begins, Fig. 7 B ( $\times 14$ ).

the leaves of *Carludovica*, that here, as in the Palms, the process by which the 'lamina' arises is rather to be described as *invagination* of the petiolar tissues. In a young leaf of *Carludovica Plumerii*, Kunth, which I examined, there was no sharp distinction between sheath (Fig. 7 A) and petiole, but

<sup>1</sup> Hirmer, M. (1919).

a series of dorsal and ventral invaginations made their appearance in the sheathing region, and, penetrating between the bundles, produced a 'plicate' form (Fig. 7 B). In the case of *C. rotundifolia*, H. Wendl., I was only able to obtain a much older leaf; in this leaf there was a well-marked cylindrical petiole, in which the process of invagination took place.

SPATHIFLORAE—Araceae.

*Calla.*

The leaves of *Calla palustris*, L., have a sheathing base enclosing the younger leaves (Fig. 8 A), continued upwards, on the ventral side, into a conspicuous *stipula adnata* (*s.a.*) (Fig. 8 B). When this stipule becomes free (Fig. 8 C), the petiole (*pet.*) assumes its definitive form. In Fig. 8 D we have reached a point above the top of the *stipula adnata*, and the two basal lobes of the cordate 'lamina' (*c.* and *c'*.) are cut across at a level below their connexion with the petiole. Fig. 8 E shows the detachment of these lobes by a pair of invaginations. In Fig. 8 F we see the 'lamina' arising by lateral winging of the petiole, while in Fig. 8 G it is completely formed. Figs. 8 H and I show its termination in a solid apex<sup>1</sup> in which all dorsiventrality is lost, and in which the bundles fuse into a vascular plexus. The solid tip of a younger leaf (*f.*<sub>2</sub>) is shown in Fig. 8 C.

*Arum.*

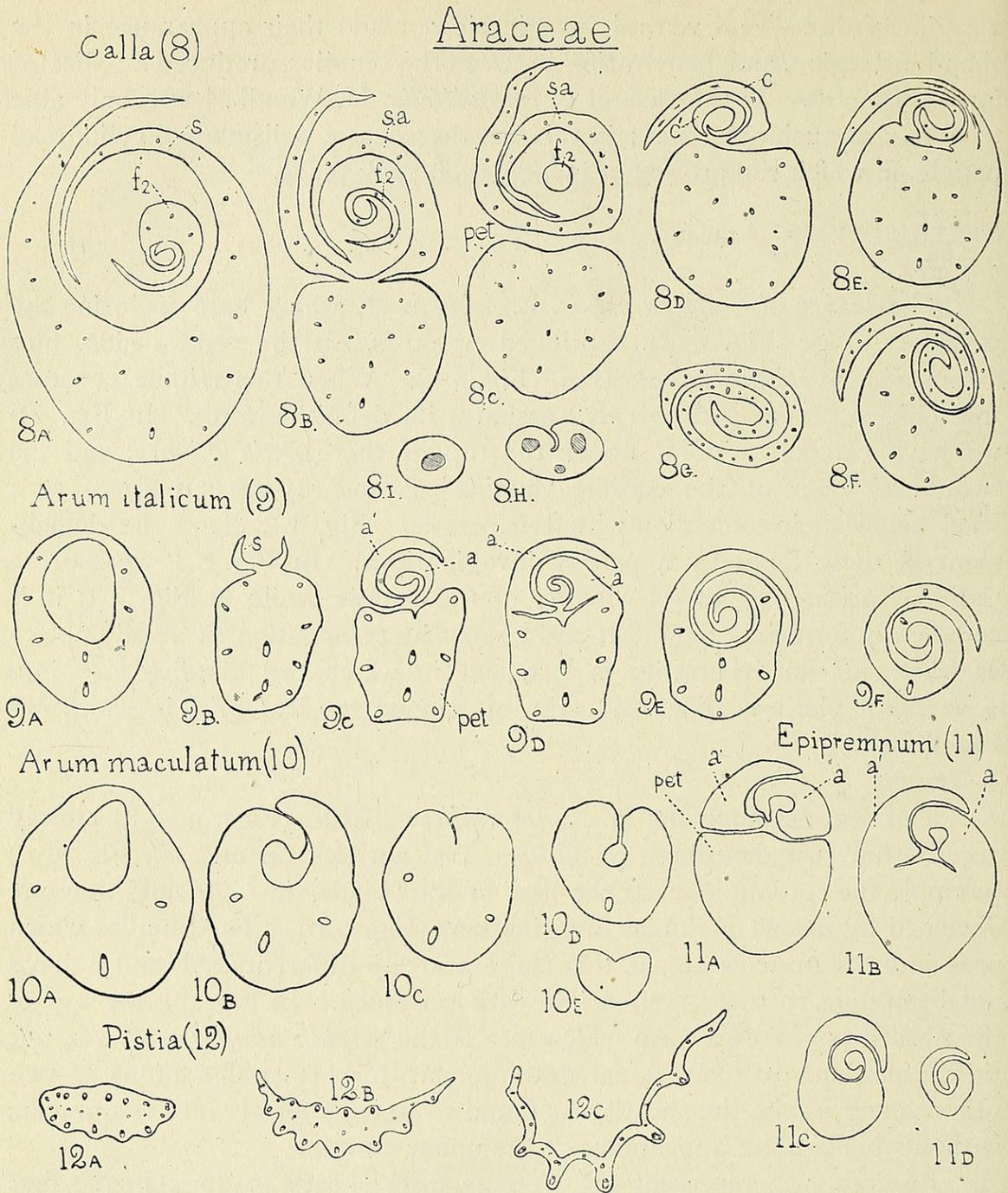
The leaf-development in *Arum italicum*, Mill. (Figs. 9 A-F) closely recalls that just described for *Calla*. The auricles (*a.* and *a'*., Fig. 9 C) resemble the cordate lobes at the base of the 'blade' in *Calla*, and they are detached by means of similar invaginations (Fig. 9 D). The bundles which pass into the auricles are at this stage scarcely differentiated, and I have not been able to trace their origin with certainty. In Fig. 9 B the top of the sheath (*s.*) takes a form which recalls the *stipula adnata* of *Calla*, but this is perhaps an exceptional development, for in serial sections of two other young leaves, the sheath was found to pass uniformly into the petiole, without this ligulate appearance at the upper margin.

Figs. 10 A-E represent the passage from sheath to apex in the first plumular leaf of *Arum maculatum*, L. This leaf is of the simple, non-auricled type, and there is a suggestion, in the transition from the petiole (Fig. 10 C) to the 'lamina' (Fig. 10 D), that invagination may play some part in the development of the latter.

*Epipremnum.*

For comparison with *Calla* and *Arum*, I cut sections through a lateral bud of *Epipremnum mirabile*, Schott, and I found that the leaf in its early stages (Figs. 11 A-D) conforms to the same type as in the two former genera. The detachment of the auricles (*a.* and *a'*., Figs. 11 A and B) and

<sup>1</sup> Arber, A. (1922<sup>2</sup>).



FIGS. 8-12. Figs. 8 A-I, *Calla palustris*, L., series of transverse sections through a young leaf ( $\times 23$ ); Fig. 8 A, sheath enclosing upper part of sheath of next leaf,  $f_2$ ; Fig. 8 B, *stipula adnata*, *s.a.*, just becoming detached; the lamina of  $f_2$  is shown; Fig. 8 C, *stipula adnata*, *s.a.*, free from petiole. *pet.*: solid apex of the second leaf,  $f_2$ , is cut through; Fig. 8 D, cordate lobes,  $c$ . and  $c'$ ., of base of 'lamina' are seen on the adaxial side of the petiole, *pet.*; Fig. 8 E, cordate lobes being detached by invagination; Figs. 8 F and G, 'lamina'; Figs. 8 H and I, solid apex of leaf, in which vascular bundles unite to a plexus (shaded). Figs. 9 A-F, *Arum italicum*, Mill., series of transverse sections through one leaf ( $\times 23$ ); Fig. 9 B passes through the extreme upper limit of the sheath,  $s$ .; Fig. 9 D shows the detachment of the auricles,  $a$ . and  $a'$ ., by means of invaginations. (Figs. 9 A-F slightly reconstructed as the sections were broken.) Figs. 10 A-E, *Arum maculatum*, L., series of transverse sections through first plumular leaf of seedling, from preparations in Miss Sargent's collection ( $\times 47$ ); Figs. 10 A and 10 B, sheath; Fig. 10 C, petiole; Fig. 10 D, 'lamina'; Fig. 10 E, solid apex. Figs. 11 A-D, *Epipremnum mirabile*, Schott, series of transverse sections through a single leaf, sheath and vascular bundles omitted ( $\times 47$ ); Fig. 11 A, just below level of attachment of auricles,  $a$ . and  $a'$ ., to petiole; Fig. 11 B, level at which auricles are connected with petiole; Figs. 11 C and D, 'lamina'. (Fig. 11 A, slightly reconstructed as section broken.) Figs. 12 A-C, *Pistia Stratiotes*, L., series of transverse sections through one young leaf ( $\times 14$ ), leaf-sheath, ligule, hairs, and lacunae, omitted; Fig. 12 A, narrow basal region; Fig. 12 C, broader distal region.

the development of the 'lamina' (Figs. 11 C and D) take place in identically the same way.

*Pistia.*

The leaf of *Pistia Stratiotes*, L., differs markedly from that of the three genera of Araceae already considered, both in its mature form and in its ontogeny. As I have described the leaf in a former paper,<sup>1</sup> and brought forward anatomical evidence for regarding it as a petiolar phyllode, I will here confine myself to the question of the origin of the thin, lamina-like, distal region of the limb. The basal part of the limb is shown in Fig. 12 A; it is solid and petiole-like. From Figs. 12 B and C it will be recognized that the development of the limb is due to a series of major dorsal invaginations and minor ventral invaginations, located between the main bundles, associated with lateral expansion of the tissue connecting the bundles.

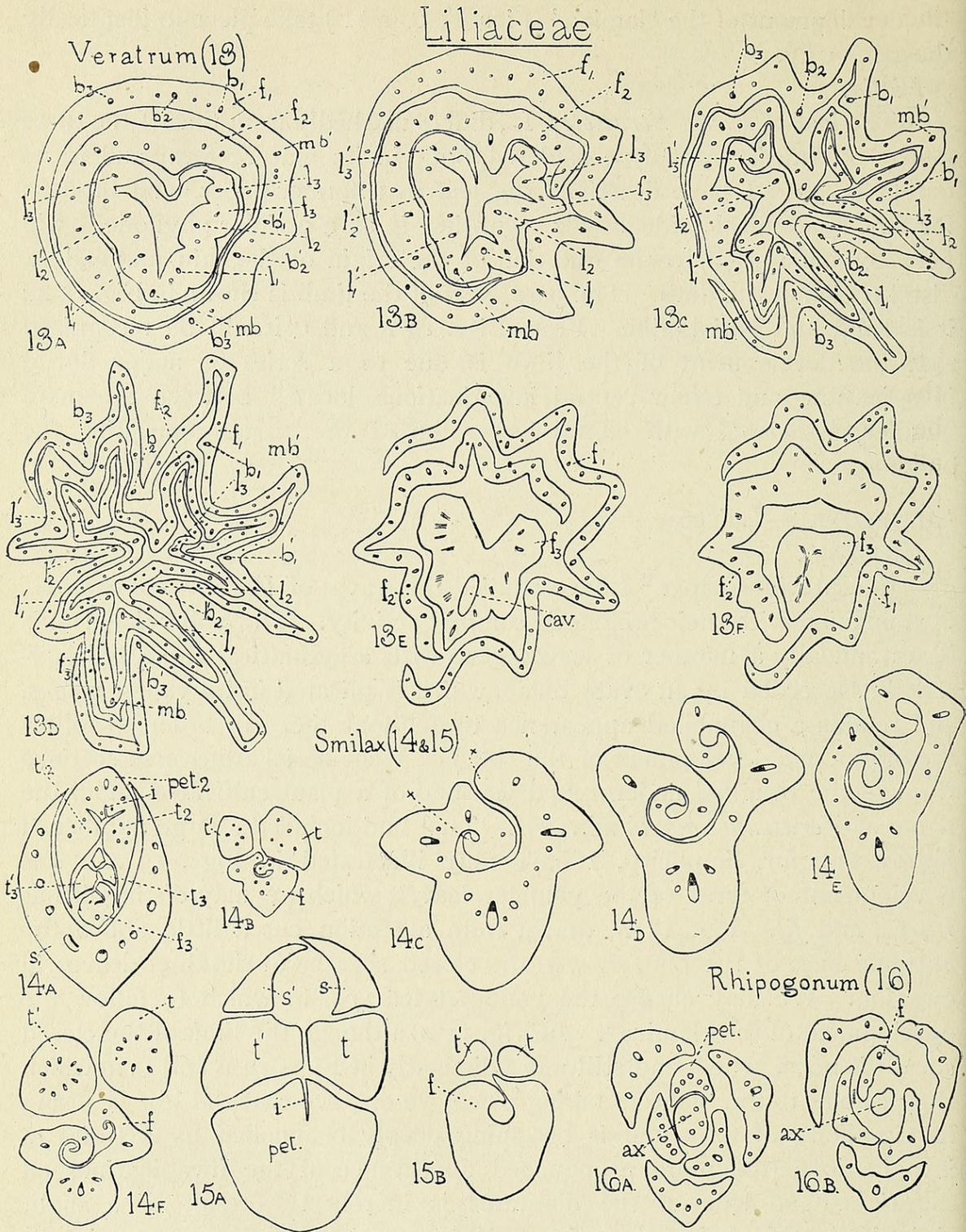
LILIFLORAE—Liliaceae.

*Veratrum.*

In a previous paper<sup>2</sup> I have studied the leaves of *Veratrum album*, L., in connexion with their prolonged cambial activity. The abbreviated axis bears annually a number of leaves, each with a cylindrical elongated leaf-sheath, succeeded by an ovate blade, which is plicated in its young stages, and retains a channelled appearance throughout life. In order to follow the origin and development of the 'blade', I cut serial transverse sections through the terminal underground leaf-bud of a plant cultivated under the name of *Veratrum 'album nigrum'*. This bud included a large number of leaves, but, for simplicity, I have only illustrated in Figs. 13 A-F the development of three of the younger leaves, which we may distinguish as  $f_1$ ,  $f_2$ , and  $f_3$ . Fig. 13 A, drawn from a section cut a little above the extreme base of the bud, showed the closed sheaths of the three leaves in question. We may choose the youngest leaf,  $f_3$ , in which to follow the development of the 'lamina'. In Fig. 13 A, although the limit of the closed sheath is not reached, and still more distinctly in Figs. 13 B and C, in which the passage to the blade is taking place, we observe that the leaf is losing its simplicity of form and is becoming deeply channelled by a series of invaginations (the more pronounced appearance of the invaginations on the right-hand side of the diagrams is merely the result of a slight obliquity in this series of sections). The positions of the grooves in the individual leaves is not haphazard, but follows a regular and definite plan. It will be recognized from Fig. 13 C that there is a dorsal invagination opposite each of the six main lateral vascular strands ( $l_1$ ,  $l_2$ ,  $l_3$ ,  $l'_1$ ,  $l'_2$ ,  $l'_3$ ) and a ventral invagination between  $l_3$  and  $l_2$ ,  $l_2$  and  $l_1$ ,  $l'_3$  and  $l'_2$ ,  $l'_2$  and  $l'_1$ , and also one between  $l_1$  and  $l'_1$ , i. e. opposite *m.b.* The result is that

<sup>1</sup> Arber, A. (1919<sup>1</sup>).

<sup>2</sup> Arber, A. (1919<sup>2</sup>).



FIGS. 13-16. Figs. 13 A-F, *Veratrum 'album nigrum'*, sections from a slightly oblique transverse series through a shoot apex, the three innermost ( $f_{11}$ ,  $f_{22}$ , and  $f_{33}$ ) of the numerous leaves being alone represented ( $\times 14$ ). Bundles of  $f_{33}$  lettered  $m.b.$  (median bundle) and  $l_{11}$ ,  $l_{22}$ ,  $l_{33}$ ,  $l'_{11}$ ,  $l'_{22}$ ,  $l'_{33}$  (lateral bundles). In Figs. 13 A, C, and D, the bundles of  $f_{11}$  are also lettered  $m.b'$  (median bundle),  $b_{11}$ ,  $b_{22}$ ,  $b_{33}$ ,  $b'_{11}$ ,  $b'_{22}$ ,  $b'_{33}$  (lateral bundles). Series ranges from Fig. 13 A, sheathing region of the three leaves, to Fig. 13 F, which passes through the solid apex of  $f_{33}$ , and near the apex of  $f_{11}$  and  $f_{22}$ ; in Fig. 13 E there is a cavity ( $cav.$ ) in  $f_{33}$ , showing that the apex is hooded. Figs. 14 A-F, *Smilax herbacea*, L., Fig. 14 A, transverse section of apical bud ( $\times 14$ ); the sheathing base of leaf  $s_{11}$  encloses a second leaf, whose petiole,  $pet_{22}$ , showing ventral invagination,  $i$ , is cut at the level of attachment of the tendrils,  $t_{22}$  and  $t'_{22}$ ; a third leaf is cut through the 'lamina',  $f_{33}$ , and the two free tendrils,  $t_{33}$  and  $t'_{33}$ ; Fig. 14 B, transverse section of another leaf passing through the lamina,  $f_{33}$ , at more

the median bundle comes to occupy the base of a channel running the length of the blade, while the main laterals,  $l_1$  and  $l'_1$ , occupy the ridges which on either side bound the median channel, and the laterals,  $l_2$  and  $l'_2$ ,  $l_3$  and  $l'_3$ , are located in the ridges separating two pairs of channels which run on either side of the median channel and parallel to it. In Figs. 13 A, C, and D I have labelled the vascular bundles in  $f_1$  as well as in  $f_3$ , in order to demonstrate that development proceeds on the same lines in both cases. In Figs. 13 C and D the median bundle of  $f_1$  ( $m.b'$ ) is seen, as in  $f_3$ , at the base of the groove between the two main laterals,  $b_1$  and  $b'_1$ , while  $b_1$ ,  $b_2$ ,  $b_3$ ,  $b'_1$ ,  $b'_2$ ,  $b'_3$ , occupy ridges separated by invaginations. That  $b_1$  is not placed at the actual summit of a ridge, is an accident due to the pressure of the more external leaves which have been omitted in the drawing. It will be noted in all three leaves that the deepening of the invaginations is associated with a thinning of the leaf-substance; this can be seen with great distinctness on comparing, for instance, the segment of the leaf  $f_1$  between the bundles  $b'_3$  and  $b'_2$ , in Figs. 13 A and D. The two bundles remain practically as fixed points, but whereas in Fig. 13 A they are connected by a simple segment of relatively thick leaf-tissue, in Fig. 13 D they have between them a deep fold, whose substance is attenuated to about one-third the thickness of the corresponding uninvaginated region in Fig. 13 A.

In Figs. 13 E and F we witness the changes which the blade undergoes in passing towards the apex. In the case of  $f_3$ , all the ventral invaginations, except the median one, have died out, while the dorsal grooves are now reduced to inconspicuous indentations. The apex is slightly hooded, so that a cavity (*cav.*) occurs in the transverse section at this level. The apex thus corresponds to that of the plicate first leaf of the Palm, *Pritchardia filifera*, Lind., which I have described elsewhere.<sup>1</sup> In Fig. 10 F the apex is solid and all the invaginations have disappeared, while the bundles, which were oblique in Fig. 13 E, are now running together, meeting one another almost horizontally.

### *Smilax.*

In a previous paper<sup>2</sup> I have considered the general morphology of the *Smilax* leaf, without, however, discussing the origin of the 'blade', the question with which we are here concerned. Serial sections through the shoot apex of *S. herbacea*, L., show that at a very early stage—in fact even before

advanced stage, and tendrils,  $t$ . and  $t'$ . ( $\times 14$ ); Figs. 14 C-E, series of sections through developing 'lamina' of another leaf ( $\times 23$ ); the points marked with a cross in Fig. 14 C will eventually become the margins of the 'lamina'; Fig. 14 F, section of another leaf ( $\times 14$ ) to show developing lamina,  $f$ ., and tendrils,  $t$ . and  $t'$ . Figs. 15 A and B, *Smilax laurifolia*, L., two sections of one young leaf ( $\times 47$ ); Fig. 15 A passes through leaf at level just above sheath and shows wings of sheath,  $s$ . and  $s'$ ., tendrils  $t$ . and  $t'$ ., and petiole,  $pet.$ , penetrated by ventral invagination,  $i$ .; Fig. 15 B, same leaf at higher level, just below tips of tendrils;  $f$ ., lamina. Figs. 16 A and B, *Rhipogonum album*, R.Br., two sections from transverse series through apical bud ( $\times 23$ );  $ax.$ , axis; the petiole,  $pet.$ , of youngest leaf is just detached in Fig. 16 A, and the same leaf is represented by the lamina,  $f$ ., in Fig. 16 B.

<sup>1</sup> Arber, A. (1922<sup>1</sup>), Fig. 5 E, p. 256.

<sup>2</sup> Arber, A. (1920<sup>2</sup>).

the tendrils separate from the petiole—the petiolar tissue begins to be penetrated by a single invagination (*i.*) passing from the ventral surface between two of the vascular bundles: This stage is seen in Fig. 14 A in the case of the petiole marked *pet.*<sub>2</sub>, to which the tendrils *t.*<sub>2</sub> and *t'*<sub>2</sub> are still attached. A little higher, where the tendrils have separated from the petiole, this invagination is found to have passed more deeply into the tissues, following a curved path, so that the future form of the 'lamina' is already indicated (*f.*<sub>3</sub> in Fig. 14 A and *f.* in Fig. 14 B). In older leaves (Figs. 14 C–F) we can follow the further development of the invagination, which—in association with a wing-like outgrowth of the two newly formed leaf margins, marked with crosses in Fig. 14 C—is responsible for the ultimate shape of the 'lamina'.

#### *Rhipogonum.*

By the kindness of Mr. J. H. Maiden, F.R.S., I have been able to examine young shoots of *Rhipogonum album*, R. Br., from the Botanic Gardens, Sidney, N.S.W. Microtome sections, through the stem apex bearing young leaves, show that in this plant the leaves have no broad basal sheath, but the petiole seems to be attached directly to the axis. This petiole passes into the 'lamina' by a gradual process—becoming broader and thinner the farther it departs from its level of attachment to the stem (cf. *pet.* in Fig. 16 A, with *f.* in Fig. 16 B). It will be recognized, on comparing Fig. 16 with Figs. 14 and 15, that both in the general ontogeny of the leaf and in the origin of the 'lamina', there are much wider divergences between *Smilax* and *Rhipogonum* than one might naturally expect, considering that the latter genus—with *Heterosmilax*—is assigned to the tribe Smilacoideae. The differences are indeed of so essential a nature as to suggest a doubt as to the close affinity assumed to exist between *Smilax* and *Rhipogonum*—a doubt which is not set at rest by a consideration of the reproductive shoots of the two genera, for *Rhipogonum* differs from *Smilax* not only in its hermaphrodite flowers, but also in the characters of the inflorescence.

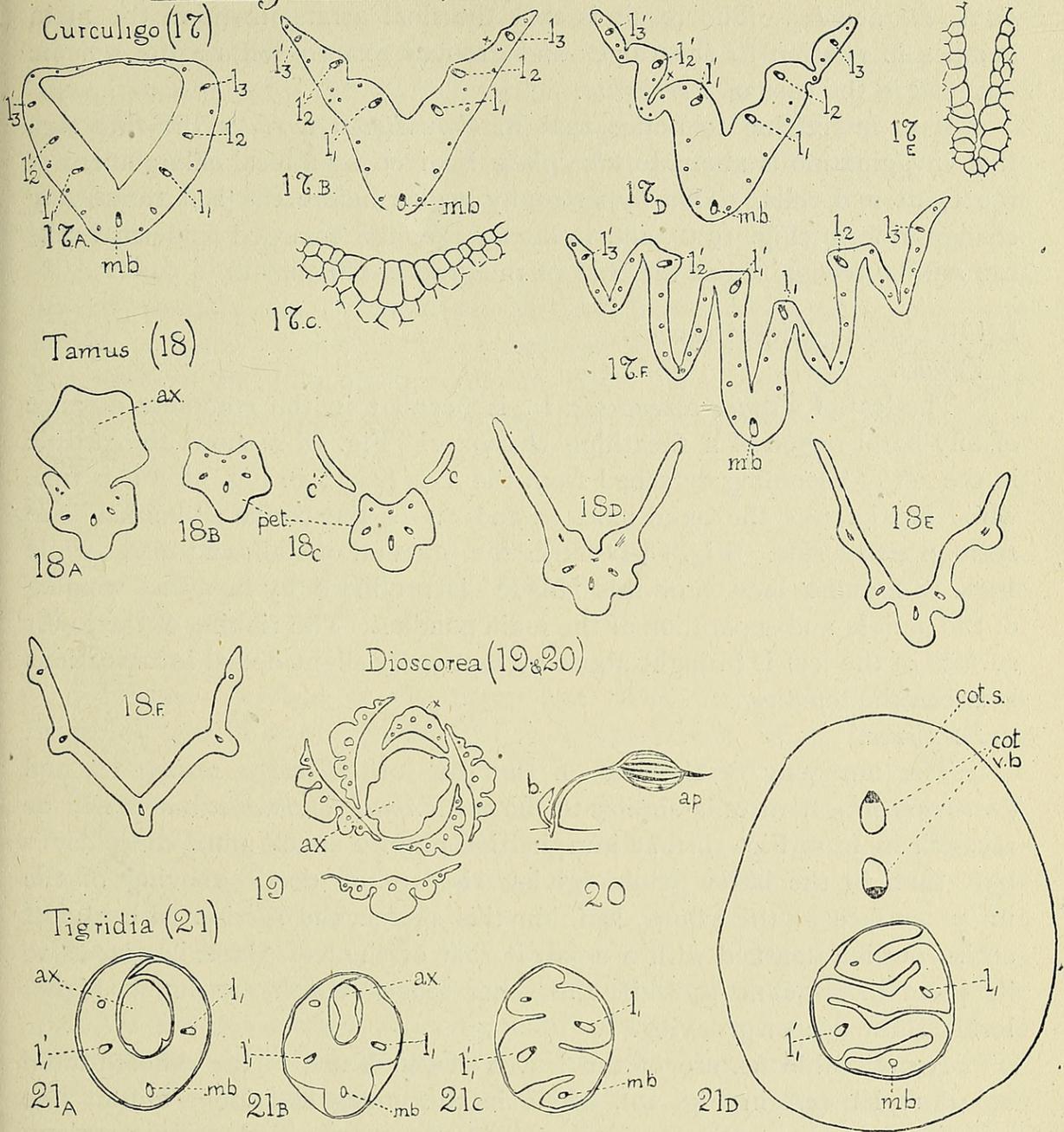
#### LILIIFLORAE—Amaryllidaceae.

##### *Curculigo.*

*Curculigo* is one of the few Monocotyledons, outside the Palms and Cyclanthaceae, which have a broad plicate leaf-limb. Just as in the case of these groups, the plicate appearance of the blade of *Curculigo* has hitherto been attributed to folding.<sup>1</sup> But, as Figs. 17 B, D, and F show, the ultimate leaf-form in *C. recurvata*, Dryand., is due, in reality, to a series of alternating dorsal and ventral invaginations of the petiole (or sheath). The 'lamina' development strikingly recalls that of *Veratrum*, already described (pp. 337–9); we find here precisely the same arrangement of a ventral sinus opposite the median bundle, *m.b.*, and four other parallel ventral

<sup>1</sup> Hirmer, M. (1919).

Amaryllidaceae, Dioscoreaceae, Iridaceae



FIGS. 17-21. Figs. 17 A-F, *Curculigo recurvata*, Dryand. Figs. 17 A, B, D, F, series of transverse sections through one leaf, passing from sheath, Fig. 17 A, to 'plicate lamina', Fig. 17 F ( $\times 14$ ); m.b., median bundle; l<sub>1</sub>, l<sub>2</sub>, l<sub>3</sub>, l'<sub>1</sub>, l'<sub>2</sub>, l'<sub>3</sub>, main laterals: Fig. 17 C, epidermis at region marked with cross in Fig. 17 B ( $\times 77$ ); Fig. 17 E, epidermis of base of groove marked with cross in Fig. 17 D ( $\times 77$ ). Figs. 18 A-F, *Tamus communis*, L., series of transverse sections through one leaf ( $\times 23$ ) passing from attachment of leaf and axis (ax., Fig. 18 A) to 'lamina' (Fig. 18 F); c. and c', cordate basal lobes of 'lamina' cut on either side of upper part of petiole, pet. Fig. 19, *Dioscorea sativa*, L., transverse section of apical bud, passing through axis, ax., and a series of leaves of which the one marked with a cross is cut nearest to its level of attachment ( $\times 14$ ). Fig. 20, *Dioscorea* sp., young leaf with axillary bud, b, to show narrow pointed apex, ap., which is becoming brown and shrivelled (about nat. size). Figs. 21 A-D, *Tigridia Pringlei*, S. Wats., sections through first plumular leaf, from sheath, Fig. 21 A, to plicate 'lamina', Fig. 21 D, from a series in Miss Sargent's collection ( $\times 47$ ). The outer line represents the inner epidermis of the cotyledon sheath (cot. s.), which is only shown completely in Fig. 21 D; ax., plumular bud; m.b., l<sub>1</sub> and l'<sub>1</sub>, main bundles of first plumular leaf; cot. v. b., vascular bundle of cotyledon, which is cut twice, as it doubles on itself.

sinuses between the main lateral bundles,  $l_1$  and  $l_2$ ,  $l_2$  and  $l_3$ ,  $l'_1$  and  $l'_2$ ,  $l'_2$  and  $l'_3$ . In addition there are, as in *Veratrum*, dorsal sinuses opposite  $l_1$ ,  $l_2$ ,  $l'_1$ , and  $l'_2$ . The result is that the final arrangement of the main bundles in relation to the ridges and grooves exactly follows the scheme outlined in the case of *Veratrum*.

It is interesting to notice that in *Curculigo recurvata* the first sign that invagination is about to take place is given by a local enlargement of the epidermal cells. This hypertrophy begins before the leaf shows any change of form (Fig. 17 C), and in later stages the enlarged epidermal cells can still be recognized at the base of the grooves (Fig. 17 E).

#### LILIIFLORAE—Dioscoreaceae.

##### *Tamus*.

The leaf of *Tamus communis*, L., is peculiar in the complete absence of any basal region of a sheathing character. Fig. 18 A shows the petiole in the act of becoming detached from the axis (*ax.*); in Fig. 18 B it is free, while in Fig. 18 C the basal lobes (*c.* and *c'.*) of the cordate 'lamina' are seen on either side. Fig. 18 D marks the junction of stalk and blade, while Figs. 18 E and F show how this 'blade' is produced by marginal winging of the petiole and separation of the main bundles. The ribbing of the lower surface of the leaf is brought about by extremely slight dorsal invaginations between the bundles.

##### *Dioscorea*.

The ontogeny of the leaf in the case of *Dioscorea sativa*, L., and *D. divaricata*, Blanco, is similar to that of *Tamus communis*, but it will be recognized from Fig. 19 that invagination plays a much more conspicuous part than in the latter genus—giving rise to the deep grooving of the under surface of the young leaf; in this sketch, the section with almost entire outline (marked with a cross) is that of the leaf which is nearest to its point of attachment, while the other leaves, which are cut at higher levels, show deeper grooving.

A noticeable feature of the leaves of the Yams is the differentiated apical region (*ap.* in Fig. 20), which in the young leaf looks almost like a separate lamina. Sir David Prain, F.R.S., was so kind as to draw my attention some years ago to this curious structure; in order to try and understand it, I have studied serial sections through leaf-buds, and I have come to the conclusion that the distal region of the *Dioscorea* leaf has no special morphological significance. It cannot, I think, be treated as a case apart; it belongs to that class of leaf-apex which Raciborski<sup>1</sup> named 'forerunner tips', and which he showed to be associated with the climbing habit, not only in the Dioscoreaceae and in *Smilax*, but also in various Dicotyledons. I find that the leaf-tips of the Yams do not differ from the

<sup>1</sup> Raciborski, M. (1900).

remainder of the limb, except in the fact that they come to maturity precociously, while the rest of the leaf is still tiny and embryonic. Their early development seems to me a phenomenon of the same order as the very early development of the tendrils in the case of *Smilax*—a peculiarity also associated with the climbing habit. The forerunner tip is the most conspicuous feature of the Yam-leaf while it is quite young, but the rest of the limb soon catches it up, and then outstrips it, so that finally it sinks into entire insignificance. But such a reversal of the order of things is not a unique occurrence; it is, indeed, by no means unusual for the proportion of parts to alter completely in the course of ontogeny. In the embryonic leaf of *Narcissus* sp., for example, the small limb forms a mere appendage of the conspicuous sheath, but at maturity the relations are reversed, and the limb is the only obvious region, while the sheath, which originally exceeded it in size, now occupies only a minute proportion of the length of the leaf.<sup>1</sup>

#### LILIIFLORAE—Iridaceae.

Since I have already dealt in this journal with the leaf-structure of the various tribes of the Iridaceae,<sup>2</sup> I will confine myself now to a single illustrative case.

##### *Tigridia*.

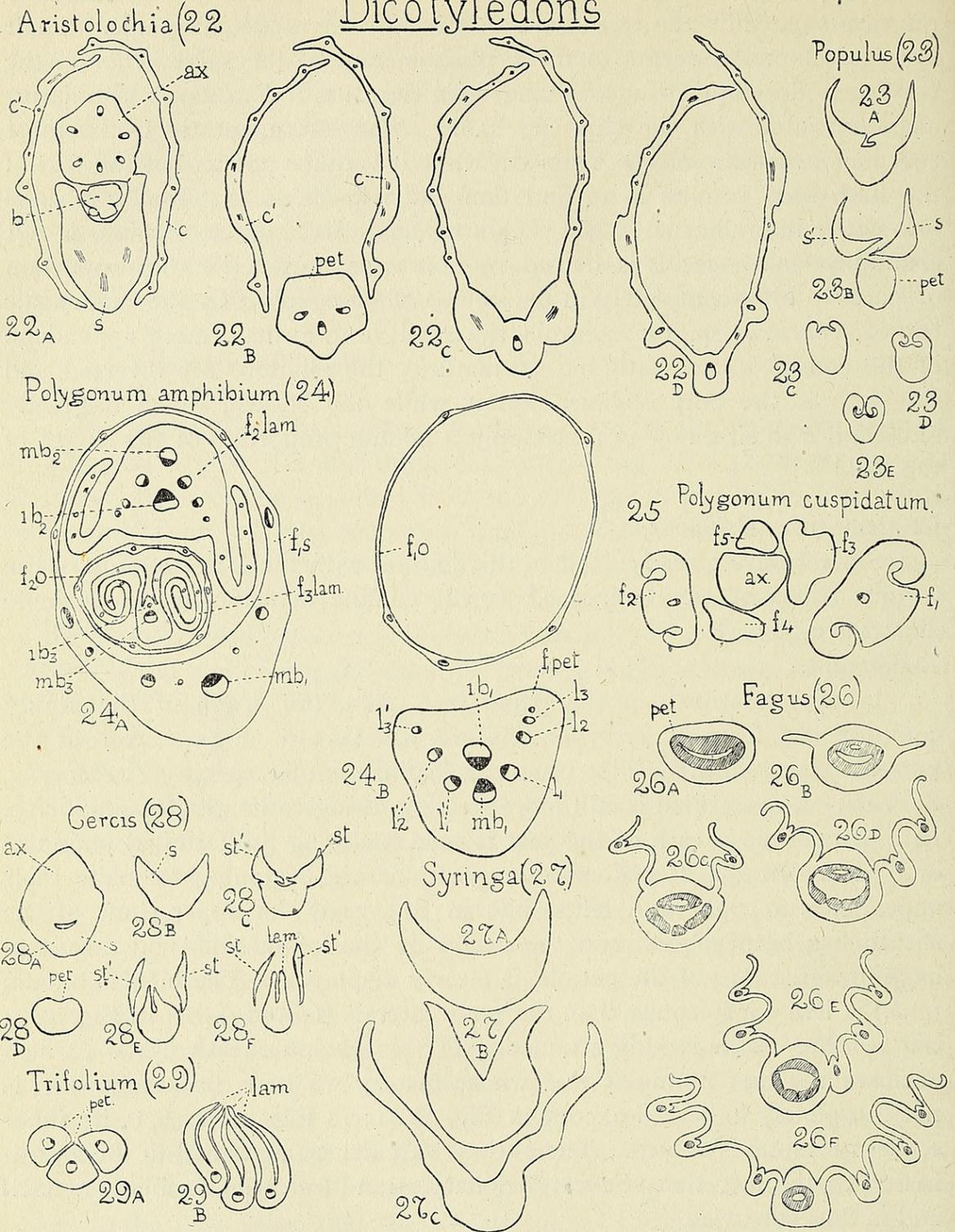
I have described, in the paper just cited, the origin of the highly complex leaf form of *Tigridia Pavonia*, Ker-Gawl.<sup>2</sup> Figs. 21 A-D of the present paper show the first plumular leaf of another species, *T. Pringlei*, S. Wats.—a case which is still more striking owing to its greater simplicity. In Fig. 21 A the sheath of this leaf is seen enclosing the terminal plumular bud (*ax.*). In Fig. 21 B dorsal invaginations are beginning to make their appearance to right and left, while in Fig. 21 C the upper limit of the sheath has been passed, and the origin of the laminations, by means of deep invaginations of the petiole, is clearly displayed. The median bundle (*m.b.*) is less conspicuous than the main laterals (*l.*<sub>1</sub> and *l'*<sub>1</sub>). In Fig. 21 D the 'plicate' form is fully attained. The cotyledon sheath (*cot. s.*), which encloses the first plumular leaf, whose history we have been following, is not completely indicated except in Fig. 21 D; in Figs. 21 A, B, C, its inner epidermis alone is shown. The curious vascular arrangement in the sheath is due to the fact that the cotyledonary strand (*cot. v.b.*) doubles on itself and is thus cut twice.<sup>3</sup>

<sup>1</sup> Arber, A. (1921<sup>3</sup>), Figs. 1 and 2, p. 103.

<sup>2</sup> Arber, A. (1921<sup>1</sup>).

<sup>3</sup> Sargent, E., and Arber, A. (1915), p. 168 and Text-fig. 8.

Dicotyledons



FIGS. 22-29. Figs. 22 A-D, *Aristolochia Clematidis*, L., series of transverse sections of a single leaf from apical bud ( $\times 23$ ); Fig. 22 A, attachment of sheathing base, *s.*, enclosing axillary bud, *b.*, to axis, *ax.*; *c.* and *c'*., bases of cordate lobes of lamina; Fig. 22 B, petiole, *pet.*; Figs. 22 C and D, lamina. Figs. 23 A-D, *Populus* sp., series of transverse sections through a very young leaf ( $\times 23$ ); Fig. 23 A, sheathing base; Fig. 23 B, stipules, *s.* and *s'*., detached from petiole, *pet.*; Figs. 23 C-E, development of lamina. Figs. 24 A and B, *Polygonum amphibium*, L. Fig. 24 A, transverse section of apical bud passing through three leaves, *f*<sub>1</sub>, *f*<sub>2</sub>, and *f*<sub>3</sub> ( $\times 23$ ); *f*<sub>1</sub>*s.*, sheath of first leaf; *m.b.*<sub>1</sub>, median bundle of first leaf; *f*<sub>2</sub> *lam.*, lamina of second leaf; *m.b.*<sub>2</sub> and *i.b.*<sub>2</sub>, median bundle and inverted bundle of second leaf; *f*<sub>2</sub> *o.*, ochrea of second leaf; *f*<sub>3</sub> *lam.*, lamina of third leaf; *m.b.*<sub>3</sub> and *i.b.*<sub>3</sub>, median bundle and inverted bundle of third leaf; Fig. 24 B, leaf I at a higher level ( $\times 23$ ); *f*<sub>1</sub> *o.*, ochrea;

### III. OBSERVATIONS ON THE ORIGIN OF THE LAMINA IN THE LEAF OF CERTAIN DICOTYLEDONS.

#### *Aristolochia.*

I have studied the structure of the young leaf of *Aristolochia Clematidis*, L., because the cordate form of the lamina and the isolation of the bundles in the axis and petiole by broad medullary rays produce a certain similarity of type to some of the Monocotyledons we have been considering. The leaf at the point of detachment from the axis (*ax.*, Fig. 22 A) has a sheathing base (*s.*) enclosing the axillary bud (*b.*). The three main leaf-bundles pursue an oblique course at this level, since they are close to their points of egress from the axis. The cordate lobes at the base of the lamina (*c.* and *c'*.) are, in the section figured, cut on either side of the leaf-base. A little higher (Fig. 22 B) the petiole (*pet.*) assumes its definitive form. Higher still (Fig. 22 C) we see the passage of the petiole into the lamina; while Fig. 22 D shows the lamina itself. The ribbing of the underside recalls the slight invagination of the lower surface of the *Tamus* leaf (Fig. 18, p. 341).

#### *Polygonum.*

The leaf of *Polygonum amphibium*, L., to some extent resembles that of *Potamogeton natans* among the Monocotyledons, and for this reason I chose it for examination. Fig. 24 A shows a transverse section of an apical bud, passing through the sheathing leaf-base (*f.<sub>1</sub> s.*) of the outer leaf (*f.<sub>1</sub>*) and the base of the lamina (*f.<sub>2</sub> lam.*) and the ochrea (*f.<sub>2</sub> o.*) of a second leaf, and also the lamina (*f.<sub>3</sub> lam.*) of a third leaf. Fig. 24 B shows the petiole (*f.<sub>1</sub> pet.*) and ochrea (*f.<sub>1</sub> o.*) into which the sheath of the first leaf seen in Fig. 24 A passes at a higher level. It will be noticed that there is a single series of bundles in the leaf-sheath, while in the petiole and lamina there is also an inverted strand (*i.b.<sub>2</sub>* and *i.b.<sub>3</sub>*, Fig. 24 A, and *i.b.<sub>1</sub>*, Fig. 24 B) opposite the median bundle. This inverted bundle arises by the fusion and subsequent branching of the lateral bundles of the sheath at a level a little below that at which the ochrea becomes free. Two of the laterals which take part in the fusion are branches of the median bundle (*m.b.<sub>1</sub>*). On passing upwards into the limb, the bundles shown in the petiole of *f.<sub>1</sub>* (Fig. 24 B) meet with the following fate: *l.<sub>3</sub>* fuses with *l.<sub>2</sub>*, and then

*f.<sub>1</sub> pet.*, petiole; *m.b.*, median bundle; *i.b.*, inverted bundle; *l.<sub>1</sub>*, *l.<sub>2</sub>*, *l.<sub>3</sub>*, *l.<sub>1</sub>*, *l.<sub>2</sub>*, *l.<sub>3</sub>*, lateral bundles. Fig. 25, *Polygonum cuspidatum*, Sieb. et Zucc., transverse section of apical bud ( $\times 47$ ), leaf sheaths and ochreas omitted, showing five leaves at successive levels and stages of development; *f.*, petiole; *f.<sub>1</sub>-f.<sub>4</sub>*, development of coiled wings of lamina; no bundles differentiated except the median strand of *f.<sub>1</sub>* and *f.<sub>2</sub>*. Figs. 26 A-F, *Fagus sylvatica*, L., series of transverse sections cut in autumn from leaves of next year's bud, showing transition from petiole (*pet.*, Fig. 26 A) to lamina (Fig. 26 F); not all from one leaf; vascular tissue shaded; xylem and phloem not distinguished. Figs. 27 A-C, *Syringa vulgaris*, L., transverse sections showing transition from extreme base of petiole (Fig. 27 A) to lamina (Fig. 27 C) ( $\times 23$ ). Figs. 28 A-F, *Cercis Siliquastrum*, L., series of transverse sections through one leaf ( $\times 23$ ); Fig. 28 A, attachment of sheath, *s.*, to axis, *ax.*; Fig. 28 B, sheath, *s.*; Fig. 28 C, detachment of stipules, *st.* and *st'*.; Fig. 28 D, petiole, stipules omitted; Figs. 28 E and F, development of lamina, *lam.* Figs. 29 A and B, *Trifolium repens*, L., sections through one leaf ( $\times 23$ ) to show origin of laminae of leaflets (*lam.*, Fig. 29 B) from petiolules (*pet.*, Fig. 29 A).

( $l_3 + l_2$ ) fuses with  $l_1$ . A comparison of the petiole ( $f_1$  *pet.*) in Fig. 24 B with the two laminae cut at different levels in Fig. 24 A ( $f_2$  *lam.* and  $f_3$  *lam.*) shows that the lamina arises as lateral marginal outgrowths from the petiole, which become coiled as they develop.

In *Polygonum cuspidatum*, Sieb. et Zucc., the development of the lamina is essentially similar. Fig. 25 shows part of a transverse section of a very young leaf-bud of this species, in which, for simplicity, the leaf-sheaths and ochreas are omitted. In the leaf  $f_5$  the petiole is cut across; in the leaves  $f_4$  and  $f_3$  the lamina is seen arising as a pair of marginal wings; in the leaves  $f_2$  and  $f_1$ , which are each old enough to show a lignified median strand, the wings of the lamina are elongating and beginning to coil.

#### *Populus.*

Serial sections of the bud of a cultivated species of Poplar (probably *Populus nigra*, L., or a related form) show, at the base of the leaf, the stipules and petiole united into a sheath (Fig. 23 A). Higher up the stipules ( $s.$  and  $s'$ .) and petiole (*pet.*) become free (Fig. 23 B). The two halves of the lamina develop—as in *Polygonum*—as outgrowths from the margins of the petiole (Fig. 23 C), which become spirally coiled (Figs. 23 D and E). But whereas the rolling is revolute in *Polygonum* it is involute in *Populus*.

#### *Fagus.*

Sections of young leaves, dissected in October from a next year's bud of the Beech, *Fagus sylvatica*, L., show that the lamina develops as a pair of flat wings, which fold in a fan-like manner as they increase in area (Figs. 26 A–F).

#### *Cercis.*

The simple, almost cordate, blade of the Judas-tree, *Cercis Siliquastrum*, L., has a sheathing base ( $s.$ , Figs. 28 A and B) from which stipules ( $st.$  and  $st'$ .) detach themselves (Fig. 28 C). The petiole shows its characteristic form in Fig. 28 D, while in Figs. 28 E and F the halves of the lamina are seen arising from the petiole as upwardly directed outgrowths.

#### *Trifolium.*

The laminae of the leaflets of the compound leaf of *Trifolium repens*, L. (Fig. 29 B), develop as outgrowths of the partial petioles (Fig. 29 A), very much as the blades of the simple leaves of *Cercis* arise from their leaf-stalks.

#### *Syringa.*

The Lilac, *Syringa vulgaris*, L., is an example of a leaf in which the petiole (Fig. 27 A) passes almost insensibly into the lamina (Fig. 27 C).

## IV. COMPARISON BETWEEN THE ONTOGENY OF THE BLADE IN MONOCOTYLEDONOUS AND DICOTYLEDONOUS LEAVES.

In the earlier part of this paper (pp. 330-43 and Figs. 1-21) I have reviewed the mode of development of a number of Monocotyledonous leaves belonging to that type—somewhat exceptional within this Class—in which there is a definite distinction between stalk and blade. In undertaking this study I have had in mind the idea that such blades are not true laminae, but represent modifications of the distal part of the petiole; and I thought that a comparison of the development of these 'pseudo-laminae' with that of the laminae of Dicotyledonous leaves might be a help in estimating what degree of validity could be claimed for this idea. It seemed to me that the severest test of the pseudo-lamina conception would be to compare the development of the Monocotyledonous leaves in question with that of Dicotyledons whose blades resemble them in type, so that a number of differences of an obvious kind would be at once eliminated. In many of those Monocotyledonous leaves which have a differentiated blade, this blade is either ovate in form (often with a tendency to the production of a cordate or auricled base), or else it is plicated in a fan-like manner. The Dicotyledons whose leaf-development has just been described (pp. 335 and 346 and Figs. 22-9) were chosen because their blades conformed to one of these types; in a few cases they were also selected for some special reason—*Aristolochia* because of Monocotyledon-like features in its anatomy, and *Polygonum* because of the resemblance in construction between the leaf of this genus, with its ochrea, and that of certain Potamogetons. The result of my observations—stated in the most general terms—is that the lamina of those Dicotyledons which I have examined arises as wing-like outgrowths from the sides of the petiole, while in some cases the petiole itself may be regarded as undergoing lateral expansion as well as winging. In certain Monocotyledons the 'lamina' arises in exactly the same way. As regards the general scheme of their development, such leaves as those of *Potamogeton* (Fig. 1, p. 331), *Hydrocharis* (Fig. 4, p. 331), *Calla* (Fig. 8, p. 336), *Rhipogonum* (Fig. 16, p. 338), and *Tamus* (Fig. 18, p. 341) are scarcely distinguishable from those of Dicotyledons. As far as these leaves are concerned, it must be admitted that the developmental evidence affords no active support to the pseudo-lamina theory; such a blade, for instance, as that of *Tamus* (Fig. 18, p. 341) recalls in its development that of *Aristolochia* (Fig. 22, p. 344), while those of *Potamogeton* (Fig. 1, p. 331) and *Aponogeton* (Fig. 3, p. 331) resemble that of *Populus* (Fig. 23, p. 344). Such negative evidence does not, however, disprove the pseudo-lamina theory, for a blade derived from a petiole in the simplest possible way—namely, by flattening, expansion, and winging—could scarcely fail to present an exact simulacrum of a true lamina.

But the uniformity of development met with in the Dicotyledons which we have described, is not paralleled among the Monocotyledons. Besides those cases to which we have just alluded, which approximate to the Dicotyledonous type, we have a number of others in which *invagination of the petiolar tissues* plays a part of greater or less importance in the formation of the blade. Such cases have a remarkably wide distribution through the Class. I have described examples in the present paper from the Palmae, Cyclanthaceae, Araceae, Liliaceae, Amaryllidaceae, Dioscoreaceae, and Iridaceae,<sup>1</sup> and I have illustrated the origin of the 'lamina' by invagination in the case of *Areca* (Fig. 5, p. 334), *Oreodoxa* (Fig. 6, p. 334), *Carludovica* (Fig. 7, p. 334), *Pistia* (Fig. 12, p. 336), *Veratrum* (Fig. 13, p. 338), *Smilax* (Figs. 14 and 15, p. 338), *Curculigo* (Fig. 17, p. 341), *Dioscorea* (Fig. 19, p. 341), and *Tigridia* (Fig. 21, p. 341). The process is perhaps most strikingly displayed in the Palms and Irids; in many cases it produces a 'plicate' form of blade. How fundamentally this 'plication' differs from the genuine folding met with in some Dicotyledons, will be realized on comparing Figs. 5 A-E, p. 334 (illustrating the formation of the plicate limb of the Palm, *Areca sapida*, by alternating invaginations which penetrate between the vascular strands of the petiole), with Figs. 26 A-F, p. 344 (illustrating the development of the Beech-leaf, *Fagus sylvatica*, in which the two halves of the lamina fold up in a delicately fan-like fashion as they increase in width). As another pair of contrasting cases we may take *Crocus* and *Polygonum*; in the *Crocus*-leaf<sup>2</sup> a couple of dorsal invaginations finally produce a revolute vernation closely similar to the arrangement of the coiled lateral wings of the leaf of *Polygonum* (Fig. 24, p. 344).

Though I have not observed invagination as a main factor in lamina development either in the Helobieae or in the Araceae (except *Pistia*), yet in the cases which I have examined from these groups in which the leaves are definitely auricled at the base (*Sagittaria* of the Alismaceae, *Calla*, *Arum*, and *Epipremnum* of the Araceae) I have found that the auricles are detached by the penetration of a deep groove, which should perhaps be classed with the invaginations met with elsewhere among Monocotyledonous leaves. These grooves in *Sagittaria* start from the dorsal surface (see arrows in Figs. 2 D and H, p. 331), whereas in *Calla*, *Arum*, and *Epipremnum* they penetrate into the leaf from the ventral side (Figs. 8 E, 9 D, and 11 B, p. 336).

From the comparison which we have instituted between the development of Monocotyledonous and Dicotyledonous laminae, I think we may conclude that, although in a number of Monocotyledonous leaves 'blade' development proceeds on lines closely similar to those followed in the case of the true laminae of Dicotyledons, yet in some cases whole families (e.g. Palmae) and in other cases individual genera within a family

<sup>1</sup> The Gramineae, which will be described in a later paper, may be added to this list.

<sup>2</sup> Arber, A. (1921<sup>1</sup>), Figs. 56 and 57, p. 324.

(e. g. *Veratrum* and *Smilax* in the Liliaceae) owe the production of their 'blades' to invagination of the distal region of the petiole or sheath, a process which does not—so far as my observations go—occur as a prime factor in the leaf development of Dicotyledons. These cases of invagination are so numerous and so widely scattered through the Class as to suggest that they have a definite phylogenetic significance, and that they represent a morphological tendency inherent in the group as a whole. I think we are justified in regarding the part played by invagination in the development of the blades of Monocotyledons as offering some confirmation of the view that these organs are pseudo-laminae.

#### V. CLASSIFICATION OF THE 'BLADES' OF MONOCOTYLEDONOUS LEAVES.

I propose, in the present section of this paper, to assume the truth of the phyllode theory, and to attempt a classification of the pseudo-laminae of Monocotyledonous leaves, based upon the factors to which they owe their development from the distal region of the petiole (or sheath). These factors are :

- (i) flattening ;
- (ii) expansion, associated with separation of bundles ;
- (iii) formation of wings or keels, which may be marginal only, or which may involve other regions of the leaf ;
- (iv) invaginations, which may be single or numerous, and which may penetrate into the leaf from either the dorsal or ventral surface, or both.

The ultimate form of the 'blade' depends, in the first instance, upon the form of the petiole from which it is derived, and, secondly, upon the developmental factor (or combination of factors) responsible for blade formation. On this basis the pseudo-laminae of Monocotyledons may be grouped as follows, according to their mode of development:—

##### I. From a petiole of more or less radial structure :

(a) By flattening and expansion alone, so that radial anatomy is retained.

(i) distal region of petiole only involved, e. g. Pontederiaceae.<sup>1</sup>

(ii) whole petiole involved, e. g. *Allium victorialis*.<sup>2</sup>

(b) By flattening and expansion, so that radial anatomy is retained, associated with dorsal and ventral invaginations, e. g. *Pistia*<sup>3</sup> (Fig. 12, p. 336).

(c) By invaginations, associated with expansion and winging ; the invaginations, though morphologically dorsal, penetrate the petiole laterally ;

<sup>1</sup> Arber, A. (1918), pp. 489-91 and Fig. 23-30.

<sup>2</sup> Arber, A. (1920<sup>3</sup>), Fig. 25, p. 457.

<sup>3</sup> Arber, A. (1919<sup>1</sup>).

practically the whole petiole is involved; e.g. various Iridaceae, such as *Cypella*.<sup>1</sup>

2. From a dorsiventral petiole, or the distal region of a leaf-sheath:

(a) Mainly by expansion, e.g. *Rhipogonum* (Fig. 16, p. 338).

(b) By winging associated with expansion, e.g. *Hydrocharis* (Fig. 4, p. 331), *Aponogeton* (Fig. 3, p. 331).

(c) By both dorsal and ventral invaginations associated with expansion, e.g. Palms (Figs. 5 and 6, p. 334), *Carludovica* (Fig. 7, p. 334), *Veratrum* (Fig. 13, p. 338), *Curculigo* (Fig. 17, p. 341).

(d) By numerous ventral invaginations, e.g. *Psamma*, and other Gramineae.<sup>2</sup>

(e) By a single ventral invagination associated with expansion and winging, e.g. *Smilax* (Figs. 14 and 15, p. 338).

(f) By numerous dorsal invaginations, associated with expansion and winging, e.g. *Dioscorea* (Fig. 19, p. 341).

(g) By two dorsal invaginations, associated with expansion and winging, e.g. *Crocus*.<sup>3</sup>

It should be noted that in the classification just outlined there is no hard-and-fast line between many of the subdivisions; the value of such a grouping lies, rather, in the picture which it offers of the great range of final form produced from the distal region of the petiole (or sheath) by the interaction, in varying proportions, of a limited number of developmental factors. The most potent of these is invagination, and it is to the very various aspects under which invagination presents itself that the remarkable series of different forms assumed by the Monocotyledonous pseudo-lamina is mainly due.

## VI. SUMMARY.

As the result of a comparative study of blade development in the leaves of Monocotyledons (pp. 330-43 and Figs. 1-21) and Dicotyledons (pp. 344-6 and Figs. 22-9) it is shown that while the 'blade' in some Monocotyledons follows a course of development indistinguishable from that of certain Dicotyledons, yet in other Monocotyledons a factor is involved which appears to play no part in the development of the leaves of Dicotyledons—namely, invagination of the tissues belonging to the petiole or sheath (pp. 347-9). A classification of the 'laminae' of Monocotyledons is suggested, based upon the factors concerned in their development. This classification brings out the fact that the great range of leaf form met with in these

<sup>1</sup> Arber, A. (1921<sup>1</sup>), Fig. 50, p. 521.

<sup>2</sup> These cases will be described in a later paper on the Glumiflorae.

<sup>3</sup> Arber, A. (1921<sup>1</sup>), Figs. 56 and 57, p. 324.

'laminae' depends primarily upon the protean forms which invagination is capable of assuming (pp. 349-50). It is concluded that the wide distribution among Monocotyledons of 'blade' formation by invagination of the distal region of the petiole or sheath, confirms the view that the leaf 'blades' of this class are pseudo-laminae.

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