The Leaf Structure of the Iridaceae, considered in Relation to the Phyllode Theory.

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With sixty-six Figures in the Text.

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I. INTRODUCTION.

THE present paper forms one of a series¹ in which I am attempting to test the validity of the phyllode theory by studying the results of its application to the leaves of various groups of Monocotyledons. In this instalment I propose to deal with the Iridaceae—that family in which, on my view, the phyllodic leaf finds perhaps its most varied and complete

¹ Arber, A. (1918), (1919¹), (1920¹), (1920²), (1920³).

expression. The thesis which I hope here to substantiate is that *the leaf of the Iridaceae has no true lamina, but represents, in every case, either a petiole and leaf-base, or a leaf-base alone.*

A considerable body of work on the leaf anatomy of the Irids already exists,¹ that of the Italian writer, Hermann Ross, being particularly thorough and detailed. But I have found that, since none of the botanists who have hitherto dealt with the subject have even considered the possibility of the leaf in question being merely a modified leaf-base and petiole, their observations seldom include answers to the particular questions to which the phyllode theory gives rise. I have, therefore, found it necessary to attempt an independent examination of the principal leaf-types met with in the Iridaceae. In this connexion I must express my gratitude, for their kindness in supplying me with material, to the Director and to the Keeper of the Herbarium, the Royal Botanic Gardens, Kew, and to the Keeper of the Department of Botany, British Museum (Nat. Hist.), and also to Professor Sir Isaac Bayley Balfour, F.R.S., Professor Béguinot, of Padua, Mr. Joseph Benbow, of La Mortola, the late M. Augustin de Candolle, of Geneva, Mr. F. J. Chittenden, Miss Mabel Cobbe, Mr. W. R. Dykes, Mr. C. C. Lacaita, Miss C. E. Larter, Mrs. J. J. Lister, Mr. R. I. Lynch, Mr. J. H. Maiden, F.R.S., of Sidney, Dr. Schonland, of Grahamstown, and Professor A. C. Seward, F.R.S. I am much indebted to Mr. W. R. Dykes and to Professor J. Bretland Farmer, F.R.S., for suggestions and criticism, and to Miss E. R. Saunders for facilities for carrying out this work in the Balfour Laboratory, Cambridge.

Regarding the classification of the Iridaceae there is considerable difference of opinion; in the present paper I have provisionally adopted the scheme used in Engler's 'Pflanzenfamilien'.²

2. ENSIFORM PETIOLAR LEAVES.

(i) *The occurrence of ensiform leaves in the Iridaceae.*

In a previous paper³ I have briefly discussed the ensiform (or isobilateral equitant) leaf, and its relation to other phyllodic types. This form of leaf—the most widespread of those met with amongst Monocotyledons which show the type of anatomy that I have interpreted as phyllodic—is characteristic of the majority of the Iridaceae;⁴ it occurs in a large proportion of the Iridoideae and Ixioidae, though not in the Crocoideae. In examining the leaves of the family in the herbarium of the British Museum (Nat. Hist.) I have seen ensiform leaves in the following genera: *Acidanthera*, *Antholyza*, *Aristea*, *Belamcanda*, *Bobartia*, *Crocasmia*,

¹ Chodat, R., and Balicka-Iwanowska, G. (1892); Balicka-Iwanowska, G. (1892-3); Ross, H. (1892-3); Lindman, C. A. M. (1899).

² Pax, F. (1888).

³ Arber, A. (1918), p. 482.

⁴ Ross, H. (1892-3).

Cypella, *Dierama*, *Diplarrhena*, *Freesia*, *Geissorhiza*, *Gladiolus*, *Hesperantha*, *Iris*, *Ixia*, *Lapeyrousia*, *Libertia*, *Marica*, *Melaspheerula*, *Micranthus*, *Moraea* (*Dietes*), *Patersonia*, *Schizostylis*, *Sisyrinchium*, *Sparaxis*, *Synnotia*, *Tapeinia*, *Tritonia*, *Watsonia*, *Witsenia*. The prevalence of the ensiform leaf, indicated by the length of this list (which is not exhaustive), seems to justify us in opening our consideration of the Iridaceae with a renewed attempt to understand this foliar type, which has been the subject of much controversy.

(ii) *Views hitherto held on the nature of the ensiform leaf.*

The anomalous character of the equitant *Iris* leaf has long been recognized; in Lyte's 'Herball' of 1578 it is compared to 'the blade of a two-edged swoorde'. It is one of the most familiar examples of the 'monofacial' leaf as opposed to the more usual flattened dorsiventral type. According to Čelakovský,¹ Velenovský,² and others,³ the ensiform leaf arises through congenital concrescence. This view has been most thoroughly and consistently elaborated by Čelakovský, who follows out and accepts all the deductions that arise logically out of his theory. He holds that the bifacial leaf is universally primary, and that all monofacial leaves are produced by concrescence of the halves, to right and left of the midrib, which were originally free and flat. He even goes so far as to suppose that all petioles came originally into existence through congenital folding and fusion of the narrowed basal region of bifacial blades. Velenovský, however, while accepting Čelakovský's view for the ensiform leaf, and even for those species of *Iris* which have a 'radial' limb, refuses to apply it to such apparently similar monofacial leaves as those of *Funcus communis*, which he interprets as due to the thickening of an originally flat blade. Goebel,⁴ on the other hand, takes a view entirely opposed to those of Čelakovský and Velenovský. He declines altogether to accept the idea of congenital concrescence, but he gives no explicit statement of his opinion as to the morphological nature of the limb. He treats it as a new wing-like outgrowth from the original leaf primordium, and, as far as one can judge from the way in which he discusses it, he seems to regard it as an organ *sui generis*.

(iii) *The ensiform leaf as a petiolar structure, and the comparison with Acacia phyllodes.*

In my 1918 paper⁵ I have put forward the view that the equitant leaf which characterizes the Irises belonging to the Sections *Apogon*, *Pogoniris*,

¹ Čelakovský, L. J. (1903).

² Velenovský, J. (1907).

³ Gray, Asa (1887); Chodat, R., and Balicka-Iwanowska, G. (1892); Balicka-Iwanowska, G. (1892-3); &c.

⁴ Goebel, K. (1905) and (1913).

⁵ Arber, A. (1918); Candolle, A. P. de (1827), recognized the leaf of *Iris* as petiolar.

Cypella, *Dierama*, *Diplarrhena*, *Freesia*, *Geissorhiza*, *Gladiolus*, *Hesperantha*, *Iris*, *Ixia*, *Lapeyrousia*, *Libertia*, *Marica*, *Melaspheerula*, *Micranthus*, *Moraea* (*Dietes*), *Patersonia*, *Schizostylis*, *Sisyrinchium*, *Sparaxis*, *Synnotia*, *Tapeinia*, *Tritonia*, *Watsonia*, *Witsenia*. The prevalence of the ensiform leaf, indicated by the length of this list (which is not exhaustive), seems to justify us in opening our consideration of the Iridaceae with a renewed attempt to understand this foliar type, which has been the subject of much controversy.

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Ensiform Leaves (Iridoideae)

FIGS. 1-14. (All figures in this paper, unless otherwise stated, are drawings of transverse sections of limbs of leaves, with the adaxial side towards the top of the page; xylem, solid black; phloem, white; fibres, dotted; *m.b.*, median bundle.) Fig. 1, *Iris Pseudacorus*, L. ($\times 7$), only principal bundles indicated; Fig. 1 A, sheath; Fig. 1 B, limb. Figs. 2-4, *Iris sibirica*, L.: Fig. 2, seedling (nat. size); s, seed; c, cotyledon; l_1 and l_2 , first and second plumar leaves. Fig. 3, transverse section of l_1 at $\times 23$. Fig. 4, transverse section second leaf of another seedling at about level y in l_2 ($\times 23$). Fig. 5, *Iris* sp., longitudinal section stem apex with young leaves; l_1 , solid limb; *sh.*, sheath ($\times 14$). Fig. 6, *Iris* sp., China ($\times 14$). Fig. 7, *Iris Kaempferi*, Sieb. ($\times 7$). Fig. 8, *Iris spuria*, L. ($\times 14$). Fig. 9, *Iris Douglasiana*, Herb. ($\times 14$), the palisade parenchyma, *pal.*, more developed on left-hand face. Fig. 10, *Iris tenuifolia*, Pall. ($\times 14$); *lac.*, lacuna crossed by trabeculae. Fig. 11, *Moraea Robinsoniana*, C. Moore et F. Muell. ($\times 14$). To economize space the section is drawn in two parts, A and B; *f.*, fibres. Fig. 12, *Moraea Macleani*, Hort.; Fig. 12 A, limb at extreme top of junction with sheath, *sh.*; *d.m.*, dorsal margin; *f.*, fibres ($\times 14$); Fig. 12 B, dorsal margin of Fig. 12 A ($\times 47$). Fig. 13, *Schizostylis coccinea*, Backh. et Harv. ($\times 7$); Fig. 13 A, sheath; Fig. 13 B, limb. Fig. 14, *Acacia pendula*, A. Cunn. ($\times 14$).

&c., did not arise by congenital concrescence, but is best regarded as a petiolar phyllode, comparable with a vertical *Acacia* phyllode, from which it differs in possessing a sheathing base. I tried to show that this view is supported by a study of the external form and internal structure, by a comparison with other 'monofacial' types, especially those met with in the Iridaceae, and also by the facts of the ontogeny as described by Goebel and Trécul. Since that paper was written, I have examined the apical bud of an *Iris* with ensiform leaves, and I have found that by dissecting it under the simple microscope I could satisfy myself that the leaves, down to one which was less than 1 mm. in its greatest dimension, showed a solid upper region distinct from the sheathing base. Fig. 5 represents a section from a microtome series passing longitudinally through a similar apical bud, in which the same distinction of solid terminal limb (*l.*) and sheathing base (*sh.*) can be recognized even in leaves whose youth is extreme. The ontogeny thus yields no evidence at all for congenital concrescence. The same is true of the seedling structure (Fig. 2), for the solid phyllodic character is already recognizable even in the first plumular leaves (Figs. 3 and 4).

Figs. 1-10 illustrate the general anatomy of various ensiform *Iris* leaves. In *Iris Pseudacorus*, L. (Figs. 1 A and B), and *I. spuria*, L. (Fig. 8), the bundles on the two sides of the leaf are equal and opposite; in *I. Kaempferi*, Sieb., which is conspicuously ribbed (Fig. 7), and *I. Douglasiana*, Herb. (Fig. 9), the bundles on either side are found to be unequal in size and somewhat irregularly disposed, while in an undetermined species from China (Fig. 6) the bundles alternate. I also include here a sketch of *I. tenuifolia*, Pall. (Fig. 10), because it has been figured by Chodat and Balicka-Iwanowska¹ as lacking a median bundle, whereas I find it to be of the normal *Iris* type in this respect.

The ensiform leaves of *Moraea Robinsoniana*, C. Moore et F. Muell., and *M. Macleai*, Hort. (Iridoideae), are represented in Figs. 11 and 12. Figs. 13 A and B show the leaf structure in the Kaffir Lily, *Schizostylis coccinea*, Backh. et Harv. (Ixioidae), which is essentially similar to that of *Iris Pseudacorus*.

In my previous paper² the phyllodes of *Acacia neriifolia*, A. Cunn., *A. scirpifolia*, Meissn., and *A. Cyclops*, A. Cunn., were figured and compared with the leaves of various Iridaceae; a further study of Acacias has shown that this comparison is even more widely applicable than was then supposed. Fig. 14 illustrates the structure of the phyllode of *Acacia pendula*, A. Cunn., which may be compared with the ensiform leaves of the genus *Iris*, especially with *I. Douglasiana* (Fig. 9). Figs. 40-4, p. 318, demonstrate the relation of *Sparaxis*, and of two ensiform species of

¹ Chodat, R., and Balicka-Iwanowska, G. (1892), Fig. 10, p. 258.

² Arber, A. (1918), Figs. 1 A and B, 2 A-D, p. 474, and Fig. 21, p. 483.

Gladiolus, to *Acacia neurophylla*, W. V. Fitz, and *A. uncinella*, Benth.; Figs. 45 and 46 show the close resemblance between *Gladiolus ornatus*, Klatt, and *Acacia incurva*, Benth., while Figs. 27 and 28, p. 311, indicate the identity in type of *Sisyrinchium junceum*, E. Mey., and *Acacia teretifolia*, Benth. The similarity of these Irid and *Acacia* leaves seems to me to supply a strong argument against the congenital concrescence view. There can obviously be no question of concrescence in *Acacia*, since here we have no sheathing base, and thus the limb cannot possibly be interpreted as arising through the fusion of the margins of such a sheath. Yet the parallelism between the very various types met with among *Acacia* phyllodes, and many of the Irid leaf forms, is too exact in all essentials to be treated as fortuitous; it appears far more likely that the same morphological interpretation applies to both. The evidence of the leaf succession in the seedling makes it certain that in many *Acacias* the leaf of the mature plant is a petiolar phyllode, and the balance of probability favours the idea that the Irid leaf should come under the same category.

(iv) *Semi-equitant leaves.*

In a previous paper¹ I drew attention, very briefly, to the case of the Liliaceous plant, *Phormium tenax*, Forst., the New Zealand Flax; further work has inclined me to an alternative interpretation of the curious leaf structure of this plant—an interpretation which I think is more likely to prove valid than the view I tentatively suggested in 1918. In *Phormium* and the related genus *Dianella*, there is, in the mature leaves, a sheathing base (*a* in Figs. 15 and 22) and a normal bifacial limb (*c* in Figs. 15 and 22), but between these parts there is a short, vertically flattened region (*b* in Figs. 15 and 22) whose structure and anatomy (Figs. 19 and 23) recall the limb—or rather the transition region between sheath and limb—in the ensiform species of *Iris*. In consequence of this peculiarity, Velenovský² describes the leaves of *Phormium* and *Dianella* as 'semi-equitant', and claims them as an obvious case of congenital concrescence. To test his view I have looked into the ontogeny of the leaf, which I find to be wholly different from that of *Iris*. The very young leaves are entirely open and sheathing (Figs. 16 and 17), and this bifacial stage, in which there is no vertical ensiform region, continues until the leaves have reached a considerable size. For instance, in a leaf a little more than 30 cm. long, the closed vertical region was found to be just beginning to differentiate itself from the sheathing base. In the seedling, also, the first plumular leaves are entirely open and sheath-like (Figs. 21 A–C). The evidence from ontogeny and from seedling structure thus appears definitely to support Velenovský's contention that we have here a genuine instance of congenital

¹ Arber, A. (1918).

² Velenovský, J. (1907).

concrecence. But the same line of evidence seems to me to indicate that the leaf of *Iris* is wholly different in its morphology from those of *Phormium* and *Dianella*, and that it does not, as Velenovský assumes, represent a case in which the congenital concrecence of *Phormium* has been carried to an

FIGS. 15-23. Figs. 15-21, *Phormium tenax*, Forst. Fig. 15, two of the younger leaves of shoot ($\times \frac{1}{2}$); the left-hand leaf is open to the base, with no concrecent region; the right-hand leaf has an open sheath at *a*, a concrecent region at *b*, and a flat limb at *c*. Fig. 16, youngest leaf of shoot in Fig. 15, open to base (slightly enlarged). Fig. 17, leaf 4 mm. high from another shoot, open to base (slightly reduced). Fig. 18, transverse section at *a* across sheathing region of right-hand leaf in Fig. 15 ($\times 9$, circa). Fig. 19, transverse section at *b* across concrecent region of right-hand leaf in Fig. 15 ($\times 9$, circa). Fig. 20, transverse section at *a* (incomplete) across limb region of right-hand leaf in Fig. 15 ($\times 9$, circa). Fig. 21 A-C, seedling; Fig. 21 A, seedling ($\times \frac{1}{2}$) *l*₁, 1st leaf; *l*₂, 2nd leaf; *sh*., sheath of cotyledon; *st*., stalk of cotyledon; *s*., seed; Fig. 21 B, transverse section of *l*₁ in Fig. 21 A, at level *x* ($\times 15$, circa); Fig. 21 C, transverse section of *l*₁ in Fig. 21 A at level *y* ($\times 15$, circa). Figs. 22 and 23, *Dianella nemorosa*, Lam. Fig. 22, leaf with sheathing region, *a*, concrecent region, *b*, and open limb, *c* (reduced). Fig. 23, transverse section of leaf in Fig. 22 at level *b*, where fusion is most complete ($\times 9$, circa).

extreme point. I look upon *Phormium* and *Dianella* as plants in which a partially 'pseudo-phyllodic' leaf structure and anatomy have been reached as a secondary modification. These two Liliaceous genera would thus be best treated at present as a case apart. It is possible that certain other 'monofacial' leaves among the Monocotyledons may also prove, on further study, to be comparable with those of *Phormium* and *Dianella*.

(v) *The association of ensiform leaf and winged axis in certain Monocotyledons and Acacias.*

A peculiarity which, in many cases among the Iridaceae, is associated with an equitant leaf, is the winging of the aerial axis in the plane of flattening of the leaf limb. In the herbarium of the British Museum (Nat. Hist.) I have observed this winging in the following genera and species:—

Aristea alata, Baker; *A. anceps*, Eckl.; *A. cladocarpa*, Baker; *A. compressa*, Buching.

Bobartia gladiata, Ker-Gawl.

Lapeyrousia abyssinica, Baker; *L. compressa*, Pourr.

Marica caerulea, Ker-Gawl.; *M. gracilis*, Herb.; *M. Northiana*, Ker-Gawl.

Sisyrinchium acre, H. Mann; *S. alatum*, Hook.; *S. angustifolium*, Mill.

(Figs. 25 C and E); *S. arizonicum*, Roth; *S. bogotense*, H. B. et K.;

S. californicum, Dryand.; *S. chilense*, Hook.; *S. convolutum*,

Nocca (Fig. 25 B); *S. distantiflorum*, Kränzl; *S. grande*, Baker;

S. hirsutum, Baker; *S. incurvatum*, Gardn. (Fig. 25 A); *S. iridifolium*,

H. B. et K.; *S. micranthum*, Cav.; *S. palmifolium*, L.;

S. restioides, Spreng.; *S. tinctorium*, H. B. et K. (Fig. 25 D);

S. vaginatum, Spreng.

When the winging is examined in detail, it is found that the leaf-base is continued downwards on either side of the true axis, from which it often remains conspicuously distinct (e.g. *Sisyrinchium incurvatum*, Gardn., Fig. 25 A). This winging is chiefly to be observed in inflorescence axes, since these are frequently the only aerial stems produced by the plants of this family. In such cases it is the spathe below the inflorescence which is continued downwards to form the wing (e.g. *Sisyrinchium tinctorium*, H. B. et K., Fig. 25 D). The sharp distinction between the cylindrical axial region (*ax.*) and the flattened foliar region (*f.*) is very noticeable in the anatomy, e.g. *Sisyrinchium angustifolium*, Mill., Figs. 25 C and E. The almost equal development of the wings on the two sides of the axis in this case, is due to the fact that the spathe forms a closed sheath round the inflorescence for some little distance above its attachment, and its downward continuation is thus capable of forming a wing both on the midrib side and on the side of the fused margins. This case may be contrasted with that of *Acorus Calamus*, L. (Aroideae), Fig. 26 A, in which the spathe is not sheathing, but is connected at the base of the spadix by a very narrow region of attachment. As a result, its downward prolongation produces a wing, but only on the side corresponding to the midrib, *m.r.* (Fig. 26 B).

Winged Axes

FIGS. 24-6. Figs. 24 A and B, *Acacia alata*, R. Br.; Fig. 24 A, shoot (nat. size) to show bases of 2-ranked phyllodes decurrent through two internodes, producing winged axis; Fig. 24 B, transverse section winged axis ($\times 28$); ax., axial region; f., foliar region; sc., fibrous hollow cylinder; o., bundles cut obliquely. Figs. 25 A-E, *Sisyrrinchium*; throughout, ax. = axis (which is indicated in solid black), and f. = foliar wing of stem; Fig. 25 A, *S. incurvatum*, Gardn. (nat. size), axis with equitant leaves (L) reduced almost to sheathing bases; Fig. 25 B, *S. convolutum*, Nocca (nat. size); Fig. 25 C, *S. angustifolium*, Mill., part of branched axis (nat. size); Fig. 25 D, *S. tinctorium*, H. B. and K., top of inflorescence axis (nat. size) with spathe, sp., and fruits, fr.; Fig. 25 E, *S. angustifolium*, Mill., transverse section winged axis ($\times 28$); mr., continuation of dorsal margin of leaf next above; sc., fibrous hollow cylinder. Figs. 26 A and B, *Acorus Calamus*, L.; Fig. 26 A, fertile axis, much reduced; spd., spadix; sp., spathe; f., winged side of axis; Fig. 26 B, transverse section winged axis below spathe ($\times 7$); mr., continuation of midrib region of spathe. The numerous small bundles lying close to the epidermis are omitted.

The interest of the winged axis, from the standpoint of the phyllode theory, lies in the fact that, just as the main features of the isobilateral equitant leaf of the Irids may be compared with those of *Acacia* phyllodes, so even the minor peculiarity of the winged axis finds a parallel among the phyllodic *Acacias*. *Acacia alata*, R. Br. (Figs. 24 A and B), has two opposite rows of reduced leaves, whose downward continuation produces a winged axis bearing a general resemblance to that of *Sisyrinchium*, &c., though the occurrence of the wing on the two sides is here due to the fact that each of the two alternating phyllode bases is decurrent through two internodes. Transverse sections show that the parallelism is not confined to mere externals (cf. Figs. 24 B and 25 E); in both cases there is a central axial region (*ax.*)—radial in structure and surrounded by a sheath of fibrous tissue—entirely distinct from the associated lateral wings (*f.*).

3. NON-ENSIFORM LEAVES IN CERTAIN IRIDOIDEAE.

(i) 'Radial' leaves in *Iris* and other *Iridoideae*, and their relation to *Acacia* phyllodes.

Within the genus *Acacia* we find every transition between phyllodes which are completely flattened in the vertical plane (Figs. 14, p. 304, and 41 and 42, p. 318)¹ and others which are cylindrical and terete (Fig. 28, p. 311).² In various *Iridoideae* we meet with the same passage from equitant leaves to others that are more nearly radial. The leaves of most *Iris*es of the *Apogon* Section are characteristically ensiform (e.g. *Iris Pseudacorus*, Figs. 1 A and B, and *I. spuria*, Fig. 8), but the genus also includes 'radial' leaves. *Iris tuberosa*, L. (*Hermodactylus tuberosus*, Mill.), is a plant in which the ensiform *Iris* leaf has been modified into a remarkable tetragonal form. Figs. 29 A–C, drawn from a microtome series, show that at the extreme base there is a closed sheath (Fig. 29 A) which opens out a little higher up (Fig. 29 B) and gradually passes into a solid limb, of diamond-shaped section (Fig. 29 C). The median strand (*m.b.*) and main laterals (*m.l.*) occupy three of the four angles, and the ventral margin (*v.r.*) can be distinguished by the fact that it has no bundle with the xylem pointing directly inwards. Higher up, in the mature part of the leaf (Fig. 29 D), we find that each of the four ribs has grown out into a slight keel, supplied as a rule by two small bundles (*b.₁* and *b.₂*) which appear to arise as branches from the main bundles. Close to the apex the fibrous strands, which occupy the angles of the leaf, become increasingly conspicuous (Fig. 29 E).

The bulbous *Iris*es of the *Tetragonae* Section (*I. reticulata*, Bieb., *I. Histrio*, Reichb., *I. Vartani*, Foster, and *I. Bakeriana*, Foster) have

¹ See also Arber, A. (1918), Fig. 2 D, p. 474, and Fig. 21, p. 483.

² Ibid., Fig. 1 B, p. 474.

'radial' leaves, with four to eight angles or ribs, more or less resembling those of *Hermodactylus*. We may take the leaf of *I. reticulata* as an example. In the case of *Hermodactylus* the leaf is fairly symmetrical about a plane passing through the dorsal and ventral margins, but in the

'Radial' Leaves in Iridoideae

FIGS. 27-30. Fig. 27, *Sisyrrinchium junceum*, E. Mey., transverse section limb of leaf; *pal.*, 3-tiered palisade parenchyma ($\times 23$). Fig. 28, *Acacia teretifolia*, Benth., transverse section phyllode; *pal.*, palisade parenchyma of about two tiers of cells ($\times 23$). Figs. 29 A-E, *Hermodactylus tuberosus*, Mill.; *ml.*, main lateral; Figs. 29 A-C, sections from microtome series through base of leaf ($\times 14$) showing transition from closed sheath through open sheath to solid limb; *vr.*, ventral ridge; Fig. 29 D, mature part of another leaf; *k.*, keel; *b₁* and *b₂*, bundles of keel; *lac.*, lacuna; Fig. 29 E, section close to apex of same leaf; *f.*, fibres; *lac.*, lacuna crossed by trabeculae. Fig. 30 A-D, *Iris reticulata*, Bieb., sections from a series through base of limb of leaf ($\times 14$). Fig. 30 A and B, sheath; Fig. 30 C, transition region; Fig. 30 D, limb showing asymmetry of the two lateral faces, *s* and *s'*, which meet at the ventral ridge, *vr.*

case of *Iris reticulata* this is not so. When the leaf is examined *in situ*, the flat surface (*s*, Fig. 30 D) has all the appearance of being an upper or ventral surface, but Figs. 30 A-D, drawn from a series of transverse sections through a leaf-base, show that the leaf is markedly asymmetrical; the ridge,

v.r., is ventral, while the unequal surfaces, *s* and *s'*, are lateral. Towards the apex the leaf becomes horny; sections show that this horniness is due to a thickening of the epidermal walls.

Sisyrinchium is another genus in which both ensiform and terete leaves occur. Fig. 27 shows the oval ribbed limb of *S. junceum*, E. Mey.;¹ it may be compared with the phyllode of *Acacia teretifolia*, Benth. (Fig. 28). The resemblance is remarkably exact, the vascular strands showing a close approximation in number and distribution.

In the genera *Trimezia* and *Bobartia* the occurrence of cylindrical junciform leaves has also been described.²

(ii) *Transitional and bifacial leaf-types in Iris and Moraea.*

The Irises to which I have hitherto referred are characterized by the unimportance of the leaf-sheath as compared with the limb—at least in the mature leaves—but in the bulbous Irises of the Section *Xiphium*, the sheath takes a more prominent place. In *Iris xiphioides*, Ehr., the English Iris, there is a cylindrical limb (*pet.*), usually of some length (Fig. 31 A), but which may be reduced to a mere trace (Fig. 31 B). I regard such a leaf as a leaf-base (*sh.*) crowned by a petiole, which may be either well developed or vestigial. The evidence on which such a view can be based is set forth in a previous paper,³ in which I have shown that the leaves of certain species of *Tulipa*, *Hyacinthus*, &c., terminate in a cylindrical apex, which by analogy with the transitional forms between the mature leaf and the bud-scale in the Dicotyledon *Fatsia*, I interpret as petiolar. In *Iris xiphioides* we have a leaf of similar morphology, which, however, reveals its nature much more obviously. The apical region of *I. xiphioides* is approximately cylindrical, and its anatomy is so nearly radial that, if transverse sections be taken through it above the sheath, it is impossible to be certain about the orientation from internal evidence. In Fig. 31 D, however, the section passes through the extreme top of the junction of sheath and limb, where the last trace of the sheath cavity, *sh.*, indicates which side is adaxial.

The related species, *Iris Xiphium*, L., the Spanish Iris, is significant because the apical limb is but little modified from the ensiform type (Fig. 32 B). Mr. W. R. Dykes⁴ has pointed out that *Iris spuria* closely resembles *I. Xiphium* in floral characters. It is interesting to find that his idea of a possible relationship between these two species, and, through them, of a connexion between the *Apogon* and *Xiphium* Sections, is confirmed by the evidence of the leaf structure; the limb of *I. Xiphium* (Fig. 32 B) is of a type which would be easily derivable from that of *I. spuria* (Fig. 8, p. 304). The facts of geographical distribution put no difficulty in the way of

¹ See Arber, A. (1918), Fig. 16 B, p. 483, for a more cylindrical leaf-type belonging to the same genus.

² Ross, H. (1892-3)

³ Arber, A. (1920¹).

⁴ Dykes, W. R. (1913).

Leaves of Iris (Sections *Xiphium* and *Juno*)

FIGS. 31-5. Figs. 31A-D, *Iris xiphioides*, Ehr.; Figs. 31A and B, apical region of two leaves seen from ventral side ($\times \frac{1}{2}$) to show variation in length of cylindrical apex (*pet.*) which terminates the bifacial region (*sh.*); Fig. 31C, transverse section bifacial region ($\times 14$); Fig. 31D, transverse section limb at uppermost limit of junction of sheath (*sh.*) and limb ($\times 14$). Figs. 32A and B, *I. Xiphium*, L.; Fig. 32A, transverse section sheath; Fig. 32B, transverse section apical limb; ($\times 14$). Fig. 33, *I. filifolia*, Boiss. ($\times 11$, circa). Figs. 34A and B, *I. Kolpakowskiana*, Regel; Fig. 34A, transverse section leaf ($\times 23$); Fig. 34B, transverse section nearer apex ($\times 24$, circa); the epidermis is thickened and papillose, but this is not shown in these diagrams. Figs. 35A and B, *I. orchoides*, Carr.; Fig. 35A, transverse section leaf ($\times 14$); Fig. 35B, midrib region of Fig. 35A ($\times 77$, circa). Note contrast between lignified fibres, f_1 , and non-lignified hypodermal fibres, f_2 .

accepting Mr. Dykes's view, since Irises of the *Spuria* group are found over the whole range of *I. Xiphium*.

In *Iris filifolia*, Boiss., another of the *Xiphium* Section, the only leaf which I was able to cut had no cylindrical apical region, but it was probably exceptional in this respect.¹ Here, as in the other members of the Section which I have examined, the median bundle is less conspicuous than the main laterals (Fig. 33, p. 313).

The rare species, *I. Kolpakowskiana*, Regel,² whose affinities are somewhat uncertain, is generally associated with the *Xiphium* Section. Its leaf is described as *Crocus*-like in external appearance, but the similarity is in reality quite superficial (contrast Figs. 34 A and B with Fig. 56 I, p. 324, representing the limb of *Crocus Tomasinianus*). The leaf is grooved on the adaxial side to the very apex; it may be regarded as consisting primarily of leaf-sheath, but as including towards the apex the region of transition to the petiolar limb which has itself been lost. It bears a certain resemblance to the dorsiventral region of the leaf of *Iris filifolia*. This resemblance is not, however, very close, and the median bundle is more developed than is usual in the *Xiphium* Section. In this point the leaf rather recalls the Irises of the *Juno* Section. As *I. Kolpakowskiana* is confined to Turkestan, it would seem more probable that its affinities would be with the *Juno* Irises, which range from the Mediterranean region to the North-west Indian frontier, than with the *Xiphiums*, which are restricted to Spain and North-west Africa; but it is evidently a somewhat isolated form.

The *Juno* Irises differ from the general *Xiphium* type in being dorsiventral to the extreme apex; that is to say, the leaf is, on my view, more reduced than that of the *Xiphium* Section, and consists merely of leaf-sheath, having lost all trace of the petiole in which it once terminated. The leaves of the *Juno* Irises may be somewhat sharply folded along the midrib, which is, as a rule, at least as important as the main laterals. *Iris orchioides*, Carr. (Figs. 35 A and B) is a typical example. It shows very distinctly the difference between the lignified fibres (f_1) associated with the phloem, and the non-lignified hypodermal fibres (f_2) which lie between the (f_1) group and the epidermis. Chodat and Balicka-Iwanowska³ have shown that the presence or absence of these hypodermal fibres is a character of considerable systematic importance.

In the closely related genus *Moraea* we find parallels both for the ensiform and bifacial leaves of *Iris*. The Section *Eumoraea* (*Dietes*) contains ensiform leaves, such as those of *Moraea Macleai*, Hort. (Fig. 12, p. 304), and *M. Robinsoniana*, C. Moore et F. Muell. (Fig. 11, p. 304), which recall those of the Irises of the *Apogon* Section, &c. But we also meet with a type of leaf which resembles that of the *Xiphium* Section in being

¹ Goebel, K. (1913), p. 285.

² Hooker, J. D. (1880).

³ Chodat, R., and Balicka-Iwanowska, G. (1892).

FIGS. 36-9. Fig. 36, *Moraea polystachya*, Ker-Gawl.; Fig. 36 A, transverse section leaf ($\times 14$); Fig. 36 B, transverse section midrib region of another leaf ($\times 47$). Fig. 37, *M. bituminosa*, Ker-Gawl., transverse section leaf ($\times 14$). Fig. 38, *M. sisyrinchium*, Ker-Gawl.; Fig. 38 A, leaf-apex seen from the ventral side ($\times \frac{1}{2}$) to show solid apex, *pet.*, and bifacial region, *sh.*; Fig. 38 B, transverse section (incomplete) of bifacial region of leaf ($\times 14$); *mr.*, midrib region; *ml.*, main lateral; Fig. 38 C, transverse section apical limb of leaf, *pet.*, in Fig. 38 A ($\times 14$); Fig. 38 D, transverse section midrib region indicated by bracket in Fig. 38 B ($\times 47$). Fig. 39, *Salvia Verbenaca*, L. (Labiateae) transverse section petiole ($\times 14$) to show absence of median bundle.

prevailingly dorsiventral, but terminating in a solid monofacial apex.¹ Figs. 37 and 36 show sections of the bifacial leaves of *M. bituminosa*, Ker-Gawl., and *M. polystachya*, Ker-Gawl. Balicka-Iwanowska² states that,

¹ Ross, H. (1892-3).

² Balicka-Iwanowska, G. (1892-3).

in *M. polystachya*, opposite the larger bundles there are smaller bundles inversely orientated. I am unable to confirm this description; I find the bundles to be all normally orientated and arranged in a single series.

The most striking peculiarity of the dorsiventral *Moraeas* is the unusual character of the midrib region. This region, in the species which I have examined, is thinner than the remainder of the leaf, and its bundles are smaller than the rest and somewhat irregularly placed. This feature is not confined to the dorsiventral species. Figs. 12 A and B, p. 304, show the absence of the median bundle in the ensiform *M. Macleani*; the shape of the leaf of this species makes the lack of midrib even more conspicuous than in the bifacial forms.

The genus *Moraea* differs from *Iris* chiefly in the absence of a perianth-tube and the fact that the stamens generally cohere. It is commonly said that the *Moraeas* are found to the south and the *Irises* to the north of the Equator. But this can only be maintained if the Barbary Nut, *Iris Sisyrinchium*, L., be ranked as a true *Iris*. This plant, which ranges from Portugal and Morocco to North-west India, resembles the *Irises* in possessing a perianth-tube, but in many other points recalls the *Moraeas*. Though Sir Michael Foster¹ placed it unhesitatingly in the genus *Iris*, and both Pax² in Engler's 'Pflanzenfamilien' and Baker³ in the 'Handbook of the Irideae' take the same line, other authorities have long held that it ought to be regarded as a *Moraea*; it was figured as '*Moraea Sisyrinchium*, the European *Moraea*', in Curtis's 'Botanical Magazine' in 1811 (vol. xxxiii, No. 1407). Mr. W. R. Dykes kindly tells me that his long study of the genus *Iris* has convinced him that this plant should be excluded from the genus and transferred to *Moraea*, which it resembles in its corm and in the sheathing leaves of the inflorescence axis, while Ross⁴ and Chodat and Balicka-Iwanowska⁵ have reached the same conclusion from the leaf anatomy, which is the point that specially concerns us here. The leaf of the Barbary Nut (Fig. 38 A) recalls some of the *Moraeas* in consisting of a flat bifacial region (leaf-base) terminating in a cylindrical apex (petiole). The apical appearance of the leaf exactly corresponds, for instance, to that of *Moraea edulis*, Ker-Gawl., as figured in Curtis's 'Botanical Magazine', vol. xvii, No. 613. The internal structure is shown in Figs. 38 B-D, and it will easily be seen that in the anatomy—especially in the peculiarities of the midrib region—there is an exact reproduction of the features of such a species as *Moraea polystachya* (Figs. 36 A and B). The leaf structure thus tends to confirm the attribution to *Moraea*.

¹ Foster, M. (1892).

² Pax, F. (1888).

³ Baker, J. G. (1892).

⁴ Ross, H. (1892-3).

⁵ Chodat, R., and Balicka-Iwanowska, G. (1892).

4. LEAVES OF THE IXIOIDEAE AND PHYLLODES OF *ACACIA*.

I showed in the genus *Iris* that the phyllodic leaves range from the vertical ensiform type to the curious 'radial', angular, or ribbed forms of *Iris reticulata*, &c. A corresponding range is characteristic of the Ixioideae. We find a series beginning with typical equitant leaves, such as those of *Sparaxis* (Fig. 40, p. 318), *Antholyza* (Fig. 49), and certain species of *Gladiolus* (Figs. 43 and 44), which can be closely paralleled with the phyllodes of such Acacias as *A. uncinella*, Benth. (Fig. 42), and *A. neurophylla*, W. V. Fitz. (Fig. 41). The pseudo-midrib¹ (*p.m.r.*), formed from the two main lateral veins, is a striking common character of these Irid and *Acacia* leaves. In addition to the ensiform species, we have also, in the genus *Gladiolus* itself, certain more aberrant forms which may be regarded as developments from the type. *Gladiolus ornatus*, Klatt, for instance (Fig. 45 B), has a leaf in which the ensiform character is becoming modified, and which shows a close resemblance to the phyllode of *Acacia incurva*, Benth. (Fig. 46). *Gladiolus tristis*, L., is a still more remarkable example, which departs to an extreme degree from the usual equitant type; the cruciform section of the limb (Fig. 48 J) does not at first sight suggest a leaf at all. Fig. 48 A shows a plant of *Gladiolus tristis* with a number of young shoots. These each bear a succession of scale leaves (*sc.*₁, *sc.*₂, *sc.*₃) followed by a foliage leaf (*f.l.*) indicated in black. The clue to the peculiarities of the leaf structure is to be found in a study of the transition from the basal sheathing region to the limb. Figs. 48 B-E show this transition in the case of the tallest foliage leaf (*f.l.*) in Fig. 48 A. At the base the leaf forms a continuous sheath (Fig. 48 B), which is ridged and furrowed, the ridges coming opposite to the bundles. A little higher, the sheath becomes open, and the ridges associated with the midrib and main laterals begin to predominate; the subsidiary ridges (*r.* and *r'*.) have altogether vanished at the higher levels represented in Figs. 48 D and E, their place being taken by the grooves *g.* and *g'*. At the same time the margins of the sheath have fused, and are represented by the fourth main ridge opposite the midrib. Figs. 48 F-J show a series of sections through another leaf, in which the loss of the subsidiary ridges *r.* and *r'* can be followed somewhat more easily than in the preceding series, and in which the ultimate form of the limb (Fig. 48 J) is also included. In connexion with each of the four main ridges a pair of lateral keels or wings (*k.* and *k'* in Figs. 48 H-J) are developed; these wings are supplied by small vascular strands. The outstanding feature of these series of sections through the leaves of *Gladiolus tristis* is that the structure of the basal region of the limb (Figs. 48 D, E, and I) at once suggests that we are dealing with a cylindrical petiolar phyllode, merely modified by four deep invaginations or grooves, associated with slight lateral wings;

¹ 'Côte médiane' of Chodat, R., and Balicka-Iwanowska, G. (1892).

FIGS. 40-9. (Throughout, *p.m.r.*, pseudo-midrib; *f.*, fibres; *f.m.*, fibrous margin.) Fig. 40, *Sparaxis pulcherrima*, Hook. ($\times 14$). Fig. 41, *Acacia neurophylla*, W. V. Fitz.; Fig. 41 A, phyllode ($\times \frac{1}{2}$); Fig. 41 B, transverse section phyllode not far from base, two upper bundles not yet united ($\times 14$); *a.p.*, assimilating parenchyma; Fig. 41 C, margin of a similar phyllode (whether dorsal or ventral uncertain) to show great development of fibres in proportion to vascular tissue. Fig. 42, *Acacia uncinella*, Benth., phyllode ($\times 14$). Fig. 43, *Gladiolus dracocephalus*, Hook. ($\times 14$). Fig. 44, *Gladiolus* sp.; Fig. 44 A, adaxial side of limb to show fibrosis of pseudo-midrib and of ventral margin ($\times 14$); Fig. 44 B, dorsal margin of sheath region to show fibrosis ($\times 47$). Fig. 45, *Gladiolus ornatus*, Klatt ($\times 47$); Fig. 45 A, sheath; Fig. 45 B, limb. Fig. 46, *Acacia incurva*, Benth., transverse section phyllode ($\times 23$) for comparison with Fig. 45. Fig. 47, apex of leaf of *Watsonia marginata*, Ker-Gawl.; fibrous rim, *f.*, which is bright yellow in herbarium material, indicated in black ($\times \frac{1}{2}$). Fig. 48, *Gladiolus tristis*, L.; Fig. 48 A, young plant ($\times \frac{1}{2}$); *sc.*, successive scale leaves; *f.l.*, foliage leaf; *c.*, corm; *r.*, roots. (Brown scale leaves have been removed from corm.) Figs. 48 B-E, series of transverse sections from base upwards through tallest leaf in Fig. 48 A, ($\times 23$); *r.*, subsidiary ridges; *g.*, grooves; *m.l.*, main lateral bundles; Figs. 48 F-J, similar series through another leaf ($\times 14$); *k.* and *k'*, keels; *r.* and *r'*, subsidiary ridges. Fig. 49, *Antholyza nervosa*, Thunb., junction of top of sheath and base of limb ($\times \frac{1}{2}$).

I think that the comparison with other Irids supports this interpretation. In the upper part of the limb (Fig. 48 J) the invaginations have become so deep that, if we only knew the leaf in this region, its phyllodic character might easily be overlooked.

The sheath of *Gladiolus tristis*, with its ridged and furrowed dorsal surface (Fig. 48 F), is an instance of a type of structure which occurs repeatedly in this family, and to which I shall refer again (p. 332) when considering the general question of the evolution of the Irid leaf.

5. FIBROSIS IN IRIDS AND ACACIAS.

An exaggerated degree of development of the fibrous strands in the leaf is characteristic of many of the Iridaceae. In certain cases the survival of these strands, especially in the basal region, provides a corm-sheath, which is sometimes continued upwards as a tuft of fibres. The most striking instance I have seen is *Antholyza nervosa*, Thunb., in which, in the case of a specimen at the flowering stage in the British Museum herbarium, the fibres are as much as 28 cm. long.

In the individual leaf, the fibrous strands generally run parallel to the bundles, between the phloem and the leaf-surface, but they may also surround and enclose the bundles. In the ensiform leaf-types they are most conspicuously developed at the dorsal and ventral margins. The fibrous rim thus produced—which is rounded in section and often, in herbarium material, bright yellow, polished, and enamel-like—is characteristically confined to the limb of the leaf, and absent from the sheath; it occurs, that is to say, in the member which I interpret as a petiolar phyllode, but not in the leaf-base. *Watsonia marginata*, Ker-Gawl. (Fig. 47), is the most striking instance I have seen; here, both on the dorsal and ventral side, the rim begins abruptly at the junction of sheath and limb. There are also many noticeable cases of marginal fibres in the genus *Gladiolus* (Figs. 43 and 44), e.g. *G. Ludwigii*, Pappe, and *G. crassifolius*, Baker, while various Irises (e.g. *Iris verna*, L., and *I. Douglasiana*, Herb., Fig. 9, p. 304), *Moraea Robinsoniana*, C. Moore et F. Muell. (Fig. 11, p. 304), *Cypella coriifolia*, Baker, and some Patersonias, show the same characteristic in varying degrees.

From the standpoint of the phyllode theory, the most suggestive feature about the fibrosis of the Irid leaf is the way in which it can be paralleled among the Acacias. The phyllode of *Acacia neurophylla*, W. V. Fitz. (Fig. 41 B), for instance, has a dorsal and ventral fibrous rim, essentially similar to that of a *Gladiolus* or a *Watsonia*. The comparison of Figs. 40, 41, 44, and 47 will show the general agreement of the marginal structure in the two families. The margin of a phyllode seems more liable to fibrous thickening than that of a lamina, possibly because the latter is characteristically attenuated, while the former—not being a true margin,

but representing merely the dorsal or ventral crest of a flattened petiole—naturally tends more to massiveness.

Not only marginal but also apical fibrousness is a common character of Irids and Acacias; the indurated apices of certain 'radial' *Acacia* phyllodes may be compared with the horny leaf-tips of *Iris reticulata*.

It is scarcely possible to cut many sections of the strongly fibrous leaves of Acacias and Irids without being impressed by the apparently excessive character of the fibrosis—excessive, that is to say, from the point of view of any purpose which it may conceivably serve in the plant's economy. The most reasonable view appears to be that the fibrosis is a process outside the plant's control, which may almost be treated as a pathological result of unsuitable conditions. Dr. A. H. Church¹ has recently suggested that the xerophyte is, as it were, embarrassed by excess of waste polysaccharides, and deposits them on its cell-walls simply to get rid of them. The conditions which bring about this excess are, on his view, the disturbance of the balance between photosynthesis and proteid synthesis, due to the inadequacy of the transpiration stream in relation to the available sunlight. The common association of fibres and phloem, and the fact that fibrosis tends to increase towards the leaf apex (e.g. *Crocus vernus*, Fig. 57 B and C., p. 324, and *Hermodactylus tuberosus*, Fig. 29 E, p. 311), may perhaps be regarded as affording some indirect support to Church's view. If his theory be accepted, any utility which may be attributed to the fibres must be regarded as an entirely secondary matter.

6. FOLIATED LEAVES IN THE IRIDOIDEAE AND IXIOIDEAE.

Some of the most aberrant leaf-types met with in the Iridaceae are those for which the names 'folia tabulata' and 'mehrflächige Blätter' have been suggested, and which I propose here to term 'foliated leaves'. As Lindman² rightly points out, these leaves do not differ fundamentally from the ensiform type, though they have been in many cases modified almost out of recognition. The least modified form is perhaps that met with in *Babiana* (Ixioidae). Fig. 50 A shows a typical plant belonging to this genus. The earlier leaves (*r.l.*₁, *r.l.*₂, *r.l.*₃) consist chiefly of sheath, with a minute limb in the case of *r.l.*₂ and *r.l.*₃. In the typical foliate leaves *l.*₁, *l.*₂, and *l.*₃ the limb becomes more and more conspicuous, while the sheath at first sight suggests a petiole. It is by no means rare in Monocotyledons to find that the ancestral loss of the leaf-blade, and the compensatory development of the petiole as a 'pseudo-lamina',³ is associated with the assumption by the sheath of petiole-like functions. Fig. 50 G shows the truncated form of the limb in another species,

¹ Church, A. H. (1919).

² Lindman, C. A. M. (1899).

³ Arber, A. (1918).

Foliated Leaves

FIGS. 50-5. (Throughout, *g*, groove; *k*, keel). Figs. 50 A-G, *Babiana*; Fig. 50 A, *Babiana* sp., young plant ($\times \frac{1}{2}$); *c*, corm; *ar*, absorptive roots; *cr*, contractile root; *l*₁, *l*₂, *l*₃, normal leaves; *s*, leaf sheath; *rl*₁, *rl*₂, *rl*₃, reduced leaves; Figs. 50 B-F, series of transverse sections through junction of sheath and limb of *l*₃ in Fig. 50 A ($\times 14$); Fig. 50 G, *Babiana cuneifolia*, Baker, limb and upper part of long leaf-sheath ($\times \frac{1}{2}$). Figs. 50 H-N, *Cypella Herberti*, Herb. ($\times 14$); Figs. 50 H-M, series of transverse sections through junction of sheath and limb in one leaf; Fig. 50 N, limb of another leaf. Figs. 51 A-D, *Herbertia pulchella*, Sweet, series through junction of sheath and limb ($\times 23$). Figs. 52 A-D, *Tigridia Pavonia*, Ker-Gawl., series of transverse sections through junction of sheath and limb ($\times 7$). Fig. 53, *Cipura paludosa*, Anbl., transverse section limb ($\times 14$). Orientation uncertain, as only a fragment of the limb was available. Fig. 54, *Phoenix dactylifera*, L., transverse section near base of first foliage leaf ($\times 14$) to show 'folding'. Fig. 55, *Curculigo* sp., transverse section small part of limb near margin; leaf can be folded up like a fan ($\times 14$).

Babiana cuneifolia, Baker. The leaf-limb in this genus gives, at first glance, the impression of being folded in a fan-like fashion, but this impression is shown to be incorrect when a series of sections is cut through the junction of sheath and limb. Figs. 50 B–F represent such a series for the case of leaf L_3 in Fig. 50 A. Fig. 50 B shows the sheath region, which is quite normal. In Fig. 50 C the limb is beginning to put in an appearance, but it is modified from the ensiform type by deep grooves or invaginations (*g.*), which occupy alternating positions to right and left. As we leave the sheath region, the grooves become more conspicuously developed (Figs. 50 D and E) until in Fig. 50 F the mature form is reached. These sections show plainly that—as Lindman¹ has already pointed out—the terms ‘*feuilles plissées*’² and ‘*foglie piegate*’³, which have been suggested for these leaves, are inadmissible. We are not dealing with a case of ‘folding’, but of invagination, which is an entirely different thing. The difference is, in fact, as fundamental as that recognized by the geologist between the case of the production of certain mountain ranges by the actual wrinkling of the earth’s crust, and the case of the carving of a system of hills and valleys, by the action of rain and rivers, out of an originally flat surface. For comparison I have included Fig. 54—a section of the basal region of a leaf of *Phoenix dactylifera*, L. (Palmae)—since this leaf has been described as offering a genuine instance of folding. It will be seen from this figure that, if the leaf were flattened out, all the bundles would be normally orientated, with xylem upwards and phloem downwards. And I have also found the same thing to be true of the ‘plicated’ leaves of *Curculigo* sp. (Amaryllidaceae, Fig. 55) and *Carludovica Plumerii*, Kunth. (Cyclanthaceae). But, on the other hand, if the leaf of *Babiana* be flattened, the bundles will still be orientated in two opposite ways, as in so many other phyllodes. I propose in later papers to consider the nature of the ‘folded’ leaves of the Palms, Cyclanthaceae, *Curculigo*, &c., and to discuss the relation of these leaves to those of the Irids.

Tigridia (Iridoideae, Figs. 52 A–D) may be taken to represent a further stage in the evolution of the foliated leaf. The transition region between sheath and limb shows that pseudo-plication arises exactly as in *Babiana*, through lateral invaginations. The form is, however, rendered a little more complicated by the development of a slight keel, *k.*, from the leaf surface in the region outside the phloem of each of the main bundles; this keel may itself contain a bundle. Similar keels are also occasionally developed in non-foliated leaves. They may, for instance, occur in connexion with the midrib of an ordinary ensiform leaf, such as that of *Tritonia*,⁴ or with the angles of a tetragonal leaf, such as that of *Hermodactylus* (Fig. 29 D,

¹ Lindman, C. A. M. (1899).

² Chodat, R., and Balicka-Iwanowska, G. (1892).

³ Ross, H. (1892–3).

⁴ Arber, A. (1918), p. 486, and Figs. 15 B and C, p. 483.

p. 311), while—outside the Iridaceae—non-vascular keels are associated with the main bundles of the plicate leaf of *Curculigo* (Fig. 55).

A further stage in the complexity of the foliated leaf is reached in *Cypella* (Figs. 50 H-N), *Herbertia* (*Alophia*¹) (Figs. 51, A-D), and *Cipura* (Fig. 53), all belonging to the Iridoideae. Here the keels (*k.*, *k'*, &c.) are developed into conspicuous lamellae, supplied by a number of bundles, and usually standing out at right angles to the plane of symmetry of each of the main vascular strands. *Cypella Herberti*, Herb., is of special interest in connexion with the phyllode theory, because, just at the junction of sheath and limb, the outline of the transverse section is almost circular (Fig. 50 K). At this stage the leaf is not unlike that of *Gladiolus tristis* at a corresponding level (Fig. 48 D, p. 318). The study of the transition from sheath to limb thus removes any difficulty which might have been felt in visualizing the limbs of both these leaves as cylindrical petioles, which at the extreme base retain some approximation to a typical petiolar structure, but higher up become rapidly modified. The final form to which the limbs attain is markedly different in the two cases (cf. Fig. 50 N, and Fig. 48 J, p. 318). Their ultimate differences depend upon the fact that *Gladiolus tristis* has only four grooves, arranged as two symmetrical pairs, while each main bundle is associated with two lateral wings, whereas *Cypella Herberti* is less symmetrically modified—the grooves, which are more numerous, are placed alternately, and there is only a single wing in connexion with each main bundle.

7. THE LEAVES OF THE CROCOIDEAE.

While the Iridoideae contains 35, and the Ixiodeae 18 genera, the third tribe of the Iridaceae, the Crocoideae, includes only the four—*Romulea*, *Crocus*, *Syringodea*, and *Galaxia*.² We may first consider the two larger genera, *Romulea* and *Crocus*. Of these *Romulea* has by far the more extensive distribution; it is found in the Mediterranean region and also in Africa (including South Africa), while in the other direction it even extends into England—*R. Columnæ*, Sebast. et Mauri, occurring near Dawlish. The genus *Crocus*, on the other hand, is not represented outside the Mediterranean region. The distribution thus indicates that *Romulea* is probably the older type, and certain structural features tend to support this view. For instance, the extreme reduction of the whole *Crocus* plant³ and the length of the flower-tube may be regarded as characters in which the genus has progressed farther than *Romulea* on the path of specialization. The leaf of *Romulea* also diverges less from the average Irid type than does

¹ This case has been studied in detail by Lindman, C. A. M. (1899).

² Pax, M. (1888), and Baker, J. G. (1892). It is possible that *Galaxia* ought to be transferred to the Iridoideae; see p. 328.

³ Church, A. H. (1908).

Leaves of Crocoideae

Crocus Tomasinianus (56)*Crocus vernus* (57)*Crocus Tomasinianus* (56)

FIGS. 56-66. (Throughout, *m.l.*, main lateral bundle; *e.l.*, external lateral bundle; *v.b.*, ventral bundle; *g1* and *g2*, grooves; *lac.*, lacuna.) Figs. 56 A-I, *Crocus Tomasinianus*, Herb.; Figs. 56 A-D, sections from microtome series through transition from sheath to limb in first foliage leaf of seedling ($\times 47$); Figs. 56 E-I, series of transverse sections through leaf of mature plant from near base upwards, not including sheath ($\times 23$); Figs. 56 E-H, basal region; Fig. 56 I, higher up. Fig. 57, *Crocus vernus*, All.; Fig. 57 A, transverse section at level corresponding to Fig. 56 H; Figs. 57 B and C, transverse section near apex ($\times 14$). Fig. 58, *Marrubium velutinum*, Sibth. et Sm. (Labiatae), transverse section petiole ($\times 14$). Fig. 59, *Crocus carpetanus*, Boiss. et Reut., transverse section leaf limb ($\times 23$). Fig. 60, *Syringodea bicolor*, Baker, transverse section leaf limb ($\times 23$). Figs. 61 A-D, *Romulea Bulbocodium*, Sebast. et Mauri, series of transverse sections through leaf ($\times 23$). Fig. 62, *R. Columnae*, Sebast. et Mauri, transverse section just at top of sheath ($\times 23$). Fig. 63, *R. rosea*, Eckl.; Fig. 63 A, transverse section just at top of sheath; Fig. 63 B, transverse section limb ($\times 23$). Fig. 64, *R. crocifolia*, Vis.; Fig. 64 A, transverse section leaf limb; Fig. 64 B, transverse section close to apex ($\times 23$). Figs. 65 A-E, *Galaxia graminea*, Thunb., series of transverse sections from sheathing base to apex; possibly 65 D and E are from a different leaf ($\times 23$). Fig. 66, *Galaxia ovata*, Thunb., transverse section limb of leaf ($\times 14$).

that of *Crocus*. So it may be well to begin our consideration of the Crocoideae by trying to make out the nature of the leaf of *Romulea*, and then to consider the relation borne to it by the highly peculiar leaf of *Crocus*.

The leaf structure of *Romulea* is illustrated in Figs. 61-4. *R. Bulbocodium*, Sebast. et Mauri, is a typical example. Here there is a sheath, closed at the base (Fig. 61 A), whose most striking feature is the relative unimportance of the median bundle (*m.b.*) as compared with the main laterals (*m.l.*). Higher up, the sheath opens out (Fig. 61 B) and the passage into the limb (Figs. 61 C and D) shows that the leaf is essentially of the ensiform type, not unlike that of *Gladiolus ornatus* (Fig. 45 B, p. 318), but modified by the presence of two pairs of grooves or invaginations, one pair (*g.*₂) lying between the median bundle and the main laterals, and the other pair (*g.*₁) between the main laterals and the ventral bundle formed by the fusion of the external lateral bundles (*e.l.*). *Romulea Columnae*, Sebast. et Mauri (Fig. 62), and *R. rosea*, Eckl. (Fig. 63), do not differ essentially from the type of *R. Bulbocodium*. One member of the genus, however, *R. crocifolia*, Vis. (Figs. 64 A and B), diverges from the *R. Bulbocodium* type in being dorsiventral to the extreme apex of the leaf.¹ I interpret the leaf of this species as a reduced form, equivalent merely to the sheathing leaf-base of the other members of the genus, the petiolar limb having been lost. *R. crocifolia* thus bears the same relation to *R. Bulbocodium* that the *Juno* Irises bear to the Irises with ensiform leaves.

The leaf of *Crocus* is described by Ross² as belonging to the dorsiventral type, and is compared by him to the aberrant *Romulea crocifolia*. Čelakovský³ and Velenovský⁴ take the same view, while Chodat and Balicka-Iwanowska⁵ expressly state that the leaf of *Crocus* is in no way comparable with that of a normal *Romulea*, and Balicka-Iwanowska,⁶ in her later paper, describes it as 'absolutely isolated among the Irideae'. My study of the anatomy and mode of origin has, however, led me to a conclusion wholly different from that of these five writers; I hope to show that *the limb of the Crocus leaf is a petiolar phyllode, strictly homologous with the leaf of such a Romulea as R. Bulbocodium*, though it is true that transverse sections of the mature leaves of the two genera (cf. Figs. 56 1 and 61 D) would scarcely suggest the possibility of any relationship between them.

We may take *Crocus Tomasinianus*, Herb., as a case for description. Figs. 56 A-D represent sections from a microtome series through the base

¹ Ross, H. (1892-3), draws attention to the dorsiventral character of *R. crocifolia*, Vis. According to Béguinot, A. (1907-9), this specific name is merely a synonym of *R. nivalis*, Klatt, but judging from a leaf from Visiani's type specimen at Padua, generously sent to me by Professor Béguinot, *R. crocifolia* is more completely dorsiventral in structure than *R. nivalis*, and the leaf anatomy certainly suggests that a separate specific name might usefully be retained.

² Ross, H. (1892-3).

³ Čelakovský, L. J. (1903).

⁴ Velenovský, J. (1907).

⁵ Chodat, R., and Balicka-Iwanowska, G. (1892).

⁶ Balicka-Iwanowska, G. (1892-3).

of the first plumular leaf of a seedling of this species. Near its attachment to the axis the sheath region is closed. This closed basal region, to which attention was long ago drawn by Irmisch,¹ being extremely short, may easily be overlooked, and it is sometimes, indeed, not typically developed; in serial sections through two shoots of *Crocus speciosus*, Bieb., I found that inextricable confusion was produced by extreme telescoping of the internodes, associated with a fusion of the leaf-bases both with one another and with the axis. The vascular anatomy of the sheath in a plumular leaf of *Crocus Tomasinianus* is shown in Fig. 56 A; the median bundle (*m.b.*) is so slightly differentiated as to be scarcely visible, consisting at this stage of a few procambial cells only. The main laterals, on the other hand, are much larger, and their xylem and phloem can already be distinguished. A second smaller pair of bundles occurs, which we may call the external laterals (*e.l.*). A little higher up two invaginations (*g.*₁) come into existence between the main lateral and external lateral bundles. The further history of these grooves can be better followed in Figs. 56 E–I, which were drawn from a series of hand-sections through the base of a mature leaf of the same species. The invaginations, which are first seen in Fig. 56 F, have developed farther in Figs. 56 G and H, and the lateral wings, thus separated from the main part of the limb, increase greatly in length by intercalary growth, and become coiled. In Fig. 56 I the final stage is reached—the unrolling of the two wings having produced the curious transverse section which characterizes the mature *Crocus* leaf. I have also studied the development of the leaf in *Crocus biflorus*, Mill., *C. speciosus*, Bieb., and *C. vernus*, All.² (Fig. 57), and I find that in each case the history is closely similar to that just traced for *C. Tomasinianus*. In *Crocus vernus* I followed the structure to the leaf-tip and found that at the apex the wings become reduced and the invaginations gradually die out (Figs. 57 B and C), so that there is an eventual return to something approaching the unmodified form of the limb.

When we turn to the comparison of *Crocus* and *Romulea*, we find that the leaves are really built on the same plan, with, however, two differences, which—though non-essential—result in a conspicuously different final form. In both genera we get a pair of grooves or invaginations (*g.*₁) arising between the main laterals (*m.l.*) and the external laterals (*e.l.*), but in *Romulea* there is an additional pair of grooves (*g.*₂) lying between the median bundle and the main laterals; this pair is unrepresented in *Crocus*. Again, in *Romulea* the external laterals (*e.l.*) approach one another and finally fuse to form a single bundle (*v.b.* in Figs. 61 D and 63 B), whereas the process of invagination and winging in *Crocus* carries the two external laterals far

¹ Irmisch, T. (1850).

² Pax, F. (1888), figures the leaf of *Crocus vernus* as possessing no midrib: this, according to my observations, is an error.

apart, so that they are eventually separated by the entire width of the flat leaf. We have already shown that the leaf of *Romulea* is but little modified from the ensiform type—that is to say, it is easily derivable from the most widespread form of petiolar phyllode. If my interpretation of the limb of *Crocus*, as precisely equivalent to that of *Romulea*, be accepted, the *Crocus* leaf must also come into the category of petiolar phyllodes; indeed, apart from the comparison with *Romulea*, the structure of the *Crocus* leaf, considered in itself, carries indications that this point of view is not too far-fetched. Fig. 56 C shows how petiole-like is the stage passed through just above the sheath region of the first plumular leaf in *C. Tomasinianus*. A comparison of Fig. 56 F and Fig. 58, again, reveals how closely the stage at which the invagination is just beginning may be compared with a certain Dicotyledonous petiole, that of *Marrubium velutinum*, Sibth. et Sm.;¹ we even get a corresponding grooving and the same conspicuous pair of main laterals; but whereas the median bundle in *Crocus* is present, though extremely reduced, in *Marrubium* it is altogether absent.

With minor variations, the type of leaf described seems to be universal in the genus *Crocus*, except in the case of two species confined to Spain, *C. carpetanus*, Boiss. et Reut., and *C. nevadensis*, Amo et Campo.² I have not been able to get material of *C. nevadensis*, but I have cut sections of *C. carpetanus*, which has a leaf differing conspicuously from that of a typical *Crocus*. There is a closed sheath at the base, which passes into a somewhat asymmetrical *bifacial* leaf, traversed by a series of bundles, alternately large and small; the dorsal surface is ridged opposite each of the larger bundles (Fig. 59). The median bundle is not, as in the other *Crocuses*, smaller than the main laterals. This leaf I regard as morphologically a leaf-sheath—the petiolar limb of the other species of *Crocus* being unrepresented. But it is very different even from the sheath region of the other *Crocuses*, and rather recalls such leaves as that of *Moraea bituminosa* (Fig. 37, p. 315). The curious isolation of the leaf anatomy, in association with certain other aberrant features of the plant to which Maw draws attention, arouses some doubt as to whether the inclusion of *C. carpetanus* in the genus *Crocus* can be justified.

The small genus *Syringodea*, which is confined to the Cape, resembles *Crocus* and differs from *Galaxia* and *Romulea*, in having no above-ground stem. Ross³ describes the structure in *S. montana*, Klatt, as dorsiventral, with a convex lower surface and concave above. I have examined *S. bicolor*, Baker, and I find that the structure corresponds in general to Ross's brief description of *S. montana*. There is no strict symmetry about a midrib, and the main laterals (*m.l.*) are larger than the median bundle (*m.b.*), which does not occupy precisely the middle line of the leaf (Fig. 60). The only *Crocus* to which such a leaf could be compared is *C. carpetanus*, and even

¹ Cf. Petit, L. (1887).² Maw, G. (1886).³ Ross, H. (1892-3).

here the resemblance is not close. *Syringodea* seems rather to belong to the type of the bifacial species of *Galaxia* and *Moraea*.

Of the genus *Galaxia*, which is also confined to the Cape, I have examined two species. One of these, *G. graminea*, Thunb. (Figs. 65 A–E), shows that lack of symmetry which we have noticed as not unusual among the Iridaceae. It has a sheath (Fig. 65 A) passing into a solid limb (Fig. 65 C), which I interpret as a petiolar phyllode. The anatomy supports this view; the structure, especially in the region near the apex (Figs. 65 D and E), recalls that of the type of ensiform leaf in which the bundles alternate. In another species, *Galaxia ovata*, Thunb. (Fig. 66), the only leaf which I have been able to examine was entirely dorsiventral, but it was probably an early leaf which had not achieved the mature form, since, according to Ross's¹ description, the leaves of this species normally terminate in a short monofacial apex. It is evidently a species in which a typical petiolar phyllode, such as that found in *Galaxia graminea*, has been reduced until it consists chiefly of the leaf-base. The median bundle is unimportant as compared with the main laterals, and the general structure resembles that of various *Moraeas*. It may be recalled that the union of the stamens of *Galaxia* into a tube is also a character in which it approaches *Moraea* and differs from the other Crocoideae. It is quite possible that the genus ought to be removed into the Iridoideae, as has been suggested by Chodat and Balicka-Iwanowska.²

8. ASYMMETRY IN CERTAIN IRID LEAVES.

A tendency to the reduction or loss of the median bundle, sometimes associated with a general lack of foliar symmetry about the adaxial-abaxial plane, is exhibited in many genera of Iridoideae and Crocoideae, though not, so far as I am aware, in the Ixioidae. In the *Xiphium* Section of the genus *Iris*, the midrib is, as a rule, insignificant in comparison with the laterals (e.g. *Iris xiphioides*, Figs. 31 C and D, p. 313). In the genus *Moraea* the midrib region is often thinner than the rest of the leaf, and traversed by several small bundles, of which sometimes no individual can be reckoned as actually median. This peculiarity is not confined to the leaf-sheath leaves (Figs. 36–8, p. 315), for there may be a complete absence of a median bundle in the dorsal region of an ensiform petiolar phyllode belonging to the genus (Figs. 12 A and B, p. 304). According to Ross's³ figures, there is also no median bundle in *Bobartia* and *Ferraria*. In the Crocoideae, *Romulea* (Figs. 61–4, p. 324), *Crocus* (Figs. 56 and 57), and *Syringodea* (Fig. 60) are characterized by median bundles which are smaller than the main laterals, while in *Galaxia* (Figs. 65 and 66, p. 324) and *Syringodea* (Fig. 60) this reduction of the median bundle is associated with a lack

¹ Ross, H. (1892–3).

² Chodat, R., and Balicka-Iwanowska, G. (1892–3).

³ Ross, H. (1892–3).

of general symmetry which makes it scarcely possible to identify a midrib. These conditions can be paralleled in the leaves of some of the Liliaceae,¹ and in certain Dicotyledonous petioles and leaf-bases. For instance, a small median bundle and larger main laterals are found in certain species of *Astelia*, *Allium*, and *Arnocrinum* (Liliaceae), and in the petiole of *Antigonon* (Polygonaceae), while the leaf-base phyllode of *Anemarrhena* (Liliaceae) and the leaf-sheath of *Foeniculum* (Umbelliferae) resemble the leaf of *Crocus carpetanus* in showing no obvious symmetry about a midrib. I do not know, however, of any cases in the Liliaceae exactly corresponding to that of the Moraeas in which there is no median bundle (e.g. *M. Macleani*, Figs. 12 A and B, p. 304, and *M. polystachya*, Figs. 36 A and B, p. 315), but the petioles of certain Labiates (*Salvia Verbenaca*, Fig. 39, p. 315, and *Marrubium velutinum*,² Fig. 58, p. 324) show a corresponding lack of a median strand.

9. THE EVOLUTIONARY HISTORY OF THE IRID LEAF.

(i) *The primitive character of the ensiform leaf-type.*

In considering the evolution of the Irid leaf, the first necessity is to arrive at some working hypothesis as to what foliar type is to be regarded as primitive for the family. As I have shown on pp. 302 and 303, the typical ensiform (isobilateral equitant) leaf is met with in more than 30 of the 57 genera, including members of both the principal tribes, Iridoideae and Ixioideae. Not only is this form of leaf characteristic of the majority of Irids, but many of the other leaf forms met with in the family—however superficially different—prove on examination (as indicated in the preceding sections of this paper) to be easily derivable from the ensiform type. Among the Liliiflorae, it is not only in the Iridaceae that the ensiform leaf occurs—it is found also in the other two great families, the Liliaceae and Amaryllidaceae. Its distribution, both within the Iridaceae and in the Liliiflorae in general, justifies us in treating it as, in all probability, representing the leaf-type of the original Irid stock. The idea is consistent with Baker's³ suggestion that *Hewardia* (of the Colchicaceae) forms 'an excellent connecting link between Liliaceae and Iridaceae'—for in this monotypic genus the leaves are ensiform.

Within the genus *Iris* itself, there seems good reason to consider the ensiform leaf-type as primitive. Such a conclusion certainly follows if we accept the deduction from Dr. Willis's 'Law of Age and Area'⁴ that, within a limited group, the more widely ranging types are likely to be the

¹ Arber, A. (1920³), pp. 449, 461, and Figs. 1 and 34.

² Petit, L. (1887); in the case of *Salvia Verbenaca* I have failed to find the small median bundle figured by Petit.

³ Baker, J. G. (1880).

⁴ Willis, J. C. (1914).

more primitive. There is no single species of *Iris*¹ covering the range of the genus, but the rhizomatous Section *Apogon*, with its ensiform leaves—to which the widely ranging *I. Pseudacorus*, L., and *I. foetidissima*, L., belong—taken as a whole, covers the entire area of distribution of the genus, from the Pacific Coast of North America in the West, to China and Japan in the East. The members of this Section far outnumber those of the other subdivisions of the genus, and their numerousness, as well as the non-bearded perianth segments, may be taken as indications of the antiquity of the type. Ensiform leaves are also typical of the other large rhizomatous Section, *Pogoniris*, as well as of several smaller Sections of the genus. The bulbous Sections, *Tetragonae*, *Xiphium*, and *Juno*, on the other hand, have a non-ensiform leaf. There seems to be some degree of probability that in the Iridaceae the rhizome may have preceded the bulb. Among the Liliaceae the two related tribes which show the most generalized characters—*Melanthoideae* and *Asphodeloideae*—are prevailingly rhizomatous; it appears likely that it is from some such Liliaceous stock that the Irids have arisen. That the bulbous Irises represent a specialized and relatively late development is also indicated by the fact that, in comparison with the rhizomatous types, they are confined to relatively restricted areas. The *Tetragonae*, whose leaves may, as I have shown, be regarded as a variant upon the ensiform type, are centred about Asia Minor and the Caucasus; the *Xiphiums*, which show transitions towards leaf-base leaves (p. 312), belong to the Iberian and North-west African regions; the *Juno* Irises, whose leaves are reduced to leaf-bases pure and simple (p. 314), though they are found from the Mediterranean to North-west India, cannot compete in range with the ensiform *Apogon* Section.

The Irises are confined to the Northern Hemisphere. That they represent a very ancient stock which has had a long time to differentiate, is indicated by the fact that the genus has a wider area of distribution than any other within the family: another point which also suggests the great age of the *Iris* type is that, with the one exception of *I. setosa*, Pall.,² all the American species are endemic. In Africa, south of the Atlas Mountains, Irises are absent, and their place is taken by the closely related genus *Moraea*, one species of which extends into Australasia. In the *Moraeas* we find typically ensiform leaves resembling those of the majority of Irises, as well as reduced leaves recalling those of the *Xiphium* Section. These two genera—*Iris* and *Moraea*—together range over almost the whole world except South America. The place of the Iridaceae, in tropical and sub-tropical America, seems to be taken by the Maricineae, of which *Marica*—

¹ On the distribution of members of the genus *Iris*, see Dykes, W. R. (1913).

² See Dykes, W. R. (1913), pp. 93, 94. This *Iris*, of which a variety of forms are known to come true from seed, occurs in Northern Asia and passes into America through Kamtschatka and Alaska. It is thus possible that it entered America in relatively recent times, though sufficiently long ago to have become differentiated in that continent into a variety of distinct types.

the largest and most widely spread genus—has an ensiform leaf. It is also significant that *Marica* is rhizomatous, whereas the other two genera, *Trimezia* and *Cypella*, are bulbous. The differences between *Iris*, *Moraea*, and *Marica* seem to be of quite subordinate importance, and I think we may reasonably regard these genera as the three modern representatives, differentiated in the Northern Hemisphere, Africa, and South America respectively, from one primaeval world-ranging Irid type,¹ and still retaining many of its generalized characters, including the ensiform leaf.

(ii) *The progression from the ensiform leaf-type.*

Under the ensiform type we must include not only the typical equitant phyllodes, such as those illustrated in Figs. 1-13, p. 304, but also the forms, such as *Sisyrinchium junceum* (Fig. 27, p. 311), which only differ in the matter of proportion from the ensiform leaf of other members of the same genus—the width being greater relatively to the distance between the dorsal and ventral margins. How easy the passage from the truly ensiform to the cylindrical types can be, is seen in the genus *Acacia*, where there are ensiform phyllodes such as *A. pendula* (Fig. 14, p. 304) and *A. uncinella* (Fig. 42, p. 318), and, at the other end of the scale, cylindrical phyllodes such as that of *A. teretifolia* (Fig. 28, p. 311). In the genus *Iris* we get a similar progression from the ensiform types, through the limb of *I. Xiphium*, with its oval section (Fig. 32 B, p. 313), to the cylindrical limb of *I. xiphioides* (Fig. 31 D, p. 313).

From the ensiform leaf—using the term in the wide sense—the course of evolution shows signs of having proceeded in two directions, the petiolar limb being either reduced in all degrees down to the point of actual elimination, or else elaborated until it sometimes forms a highly complex pseudo-lamina.

The leaf-bases of equitant leaves in many cases show a marked capacity for development: for instance, in *Micranthus alopecuroides*, Eckl., the leaf-sheaths may be extremely long. In certain genera the leaf-sheath is so far developed as to play the more conspicuous rôle, while the petiolar limb either remains as a well-marked organ or is reduced to a mere vestige. In a previous paper² I have discussed the occurrence of such leaves in the Liliaceae; in the Iridaceae instances are found in the genera *Iris* (*Xiphium* Section) (p. 312), *Moraea* (pp. 314-15), *Homeria*, *Hexaglottis*, and *Galaxia*.³ In the literature, these cases are not referred to in the terms of the phyllode theory which I have here employed, but the leaves are merely described, non-committally, as bifacial with a monofacial apex.

In the *Juno* Irises reduction has gone still farther and the leaves are

¹ For an exposition of the view that all the great families of flowering plants have passed through a period when they existed in an undifferentiated world-ranging form, see Guppy, H. B. (1919).
² Arber, A. (1920¹).
³ Ross, H. (1892-3).

exclusively of leaf-base nature. In this Section the bristle-like inner perianth segments also suggest reduction-specialization. It should be recognized that the passage from the petiolar phyllode to the leaf-base leaf, though *morphologically* a reduction, may, from the standpoint of *function*, represent an advance. The leaf-bases of the *Juno* Irises, for instance, approach more nearly to true laminae, in structure and orientation, than do the petiolar phyllodes of the rest of the genus. The approximation to a normal Dicotyledonous blade, reached on this line of progression by the *loss* of the petiole and the exaggeration of the leaf-base, is arrived at on the second line of progression by a converse process—namely, *elaboration* of the petiole; by increase of surface relatively to sectional area, the limb is modified into a pseudo-lamina, which is a more powerful instrument for performing the work of the leaf. This elaboration seems to depend essentially upon invagination or grooving, which may or may not be associated with the production of keels or wings. Grooving of the leaf-tissue between the bundles is highly characteristic of the family; it occurs conspicuously in the leaf-base leaves of *Crocus carpetanus* (Fig. 59, p. 324) and *Moraea bituminosa* (Fig. 37, p. 315), as well as in various petiolar leaves. In the latter the invagination may be so slight as to result merely in a series of ribs and channels, such as those seen in *Iris xiphioides* (Figs. 31 C and D, p. 313) and *Romulea* (Figs. 61–3, p. 324), or it may go much farther, and, as we have seen in the section on Foliated Leaves (pp. 320–3, and Figs. 50–3, p. 321), it may produce the curious pseudo-plicate winged leaves of *Cypella*, &c. Even the anomalous leaves of *Crocus* are susceptible, as I have shown on p. 325, of explanation on the same lines. The changes which take place in the petiolar phyllodes of the Irids, in their effort—if we may use the term—to become more effective assimilating organs, recall the peculiar stem developments which arise in the succulent Cactaceae and Euphorbias when the axis takes on the work normally accomplished by the leaf; in both cases we find corresponding morphological changes associated with the assumption, by a radial or approximately radial organ, of work which requires a large surface. The remarkable winged stem of *Euphorbia grandicornis*, which, as Goebel¹ points out, exposes a surface scarcely inferior to that of a leafy shoot, may be broadly compared with the foliated petiolar phyllode of *Cypella* or *Herbertia*, which forms an organ in which the ratio of surface to volume must be greater than in many normal laminae.

The ingeniously diversified leaf-forms of the Iridaceae afford an illustration of the principle which I have termed the Law of Loss.² On the phyllode theory, the leaf of the ancestral Irid, in common with other primaeval Monocotyledons, was of a type, in which the lamina had been entirely eliminated, and, on the Law of Loss, this lamina having been once

¹ Goebel, K. (1889).

² Arber, A. (1919²).

discarded, could never be regained. A review of the Irid leaves leads us to the conclusion that there has been, as it were, an effort in this family to find some substitute for the lost lamina which would be more efficient than the typical petiolar phyllode as an organ of assimilation. The members of the family have all had the same problem to solve, and the same material—the petiolar phyllode—to work upon; they have apparently discovered no methods by which to deal with the situation, except invagination and the development of keels or wings. But we have only to compare the mature leaves of such divergent types as *Gladiolus tristis* (Fig. 48 J, p. 318), *Crocus* (Fig. 56 I, p. 324), and *Cypella* (Fig. 50 N, p. 321), to see what strikingly different results have been attained by the various modes in which these monotonous methods have been applied.

In surveying the whole range of Irid leaf forms, one can scarcely fail to be struck by the more or less parallel developments from the ensiform type which have recurred within different tribes and genera. In the Iridoideae we meet, in the genus *Iris*, with ensiform and 'radial' phyllodes, and also with leaf-base leaves; with both ensiform and cylindrical phyllodes in each of the genera *Sisyrinchium*, *Trimezia*, and *Bobartia*; with foliated leaves in *Cipura*, *Cypella*, and *Tigridia*. In the Ixioideae there are many ensiform leaves, such as those of *Schizostylis*; ensiform leaves and also approximately radial phyllodes in *Gladiolus*; foliated leaves in *Babiana*. A corresponding series of 'Parallelbildungen' has been recognized in the different genera of Cactaceae; Ganong¹ enumerates a number of characters which recur repeatedly in different lines within the family. One is reminded also of the 'phyletic drift' recognized by Bower² in the case of the ferns.

10. SUMMARY.

In the present paper a general examination of the leaf structure of the Iridaceae is undertaken, in order to see how far the view can be substantiated that the leaf in this family is a *phyllode*, possessing no lamina but consisting of *petiole and leaf-base*, or *leaf-base alone*. It is found that a study of the transition region between sheath and limb often throws light on the morphology of the leaf.

The ensiform (equitant isobilateral) leaf is first discussed, and the conclusion is reached that the evidence—especially the comparison with modified leaves in the genus *Acacia*—negatives the congenital concrescence theory, and points to the ensiform leaf being a petiolar phyllode (pp. 303-6). The semi-equitant leaves of *Phormium* and *Dianella* (Liliaceae) are held not to be comparable with the ensiform leaves of the Iridaceae, but to have attained their curious form as a secondary modification (pp. 306-7). It is shown that not only are ensiform leaves in many respects similar to *Acacia*

¹ Ganong W. F. (1894)

² Bower, F. O. (1918).

phyllodes, but even the minor detail of the association of ensiform leaves and winged axes, sometimes met with in the Iridaceae and other Monocotyledons, can be paralleled in the genus *Acacia* (pp. 308-10). The nature of the 'radial leaves' of *Hermodactylus*, certain species of *Iris*, &c., is discussed, and it is shown that these leaves are merely variants upon the ensiform type (pp. 310-12); and that they lead on to the leaves of certain Irises and Moraeas, which are mainly dorsiventral, but have a monofacial apex; such leaves are regarded as leaf-bases terminating in a more or less vestigial petiole (pp. 312-16). The leaves of the *Juno* Irises are interpreted as being exclusively of leaf-base nature (p. 314). The leaves of the Ixioideae are next considered, and the origin of the cruciform leaf of *Gladiolus tristis* is traced in detail. It is shown that all such leaves are again mere modifications of the ensiform type, and that the leaves of various species of *Gladiolus* can be paralleled within the genus *Acacia* (pp. 317-19). Attention is drawn to the resemblance which many Irises and Acacias bear to one another in their tendency to excessive foliar fibrosis, and the significance of this is considered (pp. 319-20). The peculiar foliated leaf-types met with in *Babiana*, *Cypella*, &c., are examined, and it is shown that they arise from a simple petiolar structure, through invaginations, sometimes associated with the development of keels or wings (pp. 320-3). The leaves of the Crocoideae then come under consideration, and it is demonstrated that the gulf hitherto supposed to separate those of *Crocus* and *Romulea* has no real existence, but that the transition from sheath to limb shows that both leaves are petiolar phyllodes of an essentially similar type and that their divergent mature forms are merely the results of differing types of invagination (pp. 323-8). It is pointed out that the tendency to reduction or loss of the median bundle, which seems inherent in the leaves of the Iridaceae, can be paralleled in certain rare cases among Dicotyledonous petioles (pp. 328-9).

Finally, the evolutionary history of the Irid leaf is discussed, and it is concluded that the ensiform petiolar phyllode is probably primary for the family, and that the various leaf-types met with at the present day are to be interpreted either as reduced from the ensiform type by the more or less complete loss of the petiolar region, or else as elaborated from this petiolar region by invagination and winging (pp. 329-33).

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