Studies in Seed Germination.

Experiments with *Cyclamen*.¹

BY

ARTHUR W. HILL, F.R.S.

With Plate XX and fifteen Figures in the Text.

THE question as to whether the seedling of *Cyclamen* is 'monocotyledonous' or 'dicotyledonous' has attracted the attention of numerous botanists, and up to the present may still be regarded as being an open one. Bernhardt² in 1832 made the suggestion that the single seed-leaf of *Cyclamen* represents two fused leaves, basing it on the analogy of the tube formed by the two cotyledons of *Dodecatheon*; Lord Avebury also observed that abnormal seedlings of *Cyclamen* may have divided leaf-blades;³ but neither of these views need be seriously considered as tending to prove that the single cotyledon of *Cyclamen* is really a double structure.

The late Miss Sargent⁴ remarked that the 'vascular structure' of *Cyclamen persicum* 'suggests very strongly that the cotyledonary member consists of two seed-leaves united into a solid tube', but, she added, 'until the structure of allied genera has been worked out no great weight can be attached to this observation'.

The main purpose of the present paper is to give an account of some experiments and observations made on several species of *Cyclamen*, which, it is considered, afford definite proof that the embryo of *Cyclamen* does possess two cotyledons, only one of which, however, under normal conditions, develops into a leafy structure.

The opinions held by the earlier botanists on the nature of the *Cyclamen* seedling have been so well summarized by Gressner⁵ that they need no further reference here. Notice, however, must be taken of

¹ Read before the Linnean Soc., June 6, 1918. See Proc. Linn. Soc., June 6, 1918.

² Bernhardt: *Linnaea*, vii, 1832, p. 578.

³ Lubbock, Sir J.: *A Contribution to our Knowledge of Seedlings*, ii, 1892, p. 184. The double-leaved seedlings were no doubt specimens in which the original lamina had been injured and had been replaced by two new laminae produced from the top of the petiole.

⁴ Sargent, E.: *A Theory of the Origin of Monocotyledons founded on the Structure of their Seedlings*. See *Ann. Bot.*, xvii, 1903, p. 76.

⁵ Gressner, H.: *Bot. Zeit.*, 1874, p. 801, with plate.

Gressner's own view (l. c., p. 837), which is that *Cyclamen* has two cotyledons. The second cotyledon, according to him, is present only as a rudiment in the mature embryo, but develops later to form the second green leaf of the plant. Hildebrand's¹ views are based on more sound observation, for he speaks of the 'second leaf' as a small protuberance and mentions that its development can be artificially hastened by the removal of the blade of the 'first' leaf (i. e. the cotyledon). But both Gressner and Hildebrand confuse the issue by referring to the 'second' leaf, for under normal conditions the embryonic rudiment or protuberance very rarely develops, and the 'second' leaf of the young seedling *Cyclamen* is actually the first plumular leaf and is similar both morphologically and physiologically to the mature leaves of the plant.

Hildebrand, like Gressner, does not distinguish clearly between the true second cotyledon and the first plumular leaf, and judging from his concluding paragraph (l. c., pp. 96, 97) he did not consider the question of any particular interest in the biology of the seedling of *Cyclamen persicum*.

The embryo of *Cyclamen persicum* is also described and figured by Schmid.² He points out that there are two cotyledons, one of which is represented only by a rudiment, but he does not follow the germination or study the fate of the rudimentary second cotyledon.

Coulter and Chamberlain,³ in their discussion of dicotyledonous embryos with a single cotyledon, are thus incorrect in stating that Schmid 'found embryos in ripe seeds of *Cyclamen persicum* with no trace of a second cotyledon'. These authors point out that in certain dicotyledonous forms there may be early abortion which may even approach suppression of one of the cotyledons; and that in consequence of this the single functional cotyledon may appear terminal and the stem-tip lateral. 'To call such cases "pseudomonocotyledons", however, is not consistent with the real nature of the monocotyledonous embryo.'⁴

No definite pronouncement is made by Goebel⁵ as to whether *cyclamen* possesses two cotyledons or only a single one. He speaks of the seedling having only a single leaf, which is followed in due course by other primary leaves of similar form, and allows it rather to be assumed that there is only a single cotyledon in this genus.

Goebel⁶ carried out an extensive series of experiments on *Cyclamen*

¹ Hildebrand, F.: Die Gattung *Cyclamen*. Jena, 1898, p. 95.

² Schmid, B.: Bot. Zeit., 1902, p. 217, Pl. IX, Figs. 45-7. The lettering given in the explanation of Fig. 47, which shows the second cotyledon rudiment, does not agree with that on the plate.

³ Coulter and Chamberlain: Morphology of Angiosperms, 1904, p. 206.

⁴ Ibid., p. 207.

⁵ Goebel: Einleitung in die experimentelle Morphologie der Pflanzen, 1908, p. 203.

⁶ Goebel: Ueber Regeneration im Pflanzenreich. Biolog. Centralbl., xxii, 1902, pp. 435-8 and pp. 481-7, with numerous text-figures. This work is shortly summarized in his Einleitung in die experimentelle Morphologie der Pflanzen, 1908, pp. 203-6.

persicum in connexion with the regeneration of the lamina from the cotyledonary petiole. His interpretation of the *Cyclamen* seedling is not very clear, but he definitely states that the genus differs from other Dicotyledons in *not* possessing two cotyledons (l. c., p. 435), but only a single seed-leaf.

It is on this single seed-leaf or cotyledon that Goebel carried out his regeneration experiments, and he makes no reference to the development of a second cotyledon. He states, however, that in all his experiments he removed 'the second leaf', but whether this second-appearing leaf was actually the second cotyledon or, more probably, the first plumular leaf is not certain. He refers to the leaves which arise after the cotyledon as the first leaves, 'Primärblätter', whatever their morphological nature may be, and there is no evidence that he distinguished between the *true* second cotyledon and the subsequent plumular leaves.

In the course of this paper I have pointed out that the regeneration of a lamina from the petiole is a peculiarity possessed by the cotyledonary petioles only, and Goebel also notes (p. 438) that he was unable to obtain regeneration with the older leaves of plants of flowering age. He appears to state, however, in a sentence,¹ the exact meaning of which is somewhat obscure, that the leaves following the 'single' cotyledon have similar powers of regeneration to that organ. These leaves, which he calls the 'Primärblätter', should be the plumular leaves, and with such I find no regeneration of the lamina takes place. Possibly he may have experimented with the *second leaf* of a seedling which did happen to be a true second cotyledon, otherwise I am unable to reconcile his conclusion.

Winkler² also, it may be mentioned, shows no particular interest in the question of the monocotyledonous or dicotyledonous character of the *Cyclamen* seedling, since his experiments are concerned with the behaviour of the first seed-leaf under traumatic stimulation, but it may be inferred from his account that he considers *Cyclamen* to be possessed of only a single cotyledon.

A preliminary account of my own experiments with reference to the development of the second cotyledon of *Cyclamen* was given at the meeting of the British Association at York in 1906.³

The *Cyclamen* seedling, as is well known, consists of a short hypocotyl—the young tuber or corm—bearing at its apex two organs placed exactly

¹ p. 438: 'Bei den Regenerationsversuchen, die oben kurz geschildert wurden, entfernte ich das zweite Blatt meist sobald es sichtbar war, übrigens verhalten sich die dem Kotyledon folgenden Blätter betreffs ihres Regenerationsvermögens ebenso wie diese' (*sic*).

² H. Winkler: Ueber die Regeneration der Blattspreite bei einigen Cyclamenarten. Ber. d. Deut. Bot. Gesellsch., xx, 1902, p. 82.

³ In the course of my experiments, which were commenced at Cambridge in 1904, I have examined the seedlings of *Cyclamen Atkinsi*, *C. balearicum*, *C. Coum*, *C. libanoticum*, *C. neapolitanum*, and *C. persicum*. Figures of the seedlings of several species of *Cyclamen* are given by Hildebrand, l. c. See A. W. Hill: The Seedlings of certain Pseudo-monocotyledons. Report Brit. Assoc. York, 1906, p. 763.

opposite one another. One of these, which has already functioned as the absorbent organ in the seed, quickly develops its lamina and becomes an assimilating leaf, while the other remains in a rudimentary condition and is a scarcely visible, curved protuberance. The single assimilating organ or cotyledonary lamina is usually more or less cordate in outline with a well-marked notched apex, and is borne on a stout petiole. The cotyledonary petiole is slightly concavo- or plano-convex, a shallow groove or furrow being noticeable on the flattened inner or adaxial side, and it is from the edges of this groove—the adaxial ridges—that new laminae may be regenerated. Under normal conditions the *Cyclamen* seedling remains in

TEXT-FIG. 1. *Cyclamen neapolitanum*. A germinating seed, showing the cotyledon petiole, c. 1, and the rudiment of the second cotyledon, c. 2.

this one-leaf stage for some time and the other rudimentary organ (the second cotyledon) ultimately shrivels and dies. When a second green leaf does develop under normal conditions in due course, it is seen to differ from the seed-leaf in the shape of its lamina and in the character of its margin and markings. Moreover this second leaf does not arise opposite to the seed-leaf, the rudimentary aborted organ being in that position, but is placed between and at right angles to the two embryonic structures. This second leaf which springs from the plumular axis is thus seen to be the first leaf of the plumule or shoot. The suppression of the short axis, owing to the geophilous habit of the genus and the consequent crowding of the developing plumular leaves, may have led to the divergent views which have

found expression as to the morphological nature of the *Cyclamen* seedling.

The seedling at this stage may be compared to that of *Abronia* (Nyctagineaceae), where in the embryo and on germination only one cotyledon is in evidence, the other being represented by a minute and very slightly developed organ.¹

The evidence as to the morphological nature of the second green leaf of *Cyclamen* afforded by its position receives some support when the anatomical structure of its petiole is compared with that of the cotyledons.

Even then doubts have been expressed as to the true character of this normally developed second leaf; but these, it is hoped, may now be considered to be finally settled by the regeneration experiments on cotyledonary and plumular leaves described in the following pages.

The development of the rudimentary curved organ at the apex of the hypocotyl—the rudiment of the second cotyledon—may be induced, as

¹ See Lubbock: On Seedlings, vol. i, p. 31, Fig. 64; he figures the embryos of *Abronia arenaria* and *A. umbellata*. According to Jepson, Gray, and Brewer, Botany of California, vol. ii, p. 3, the embryo in the genus *Abronia* is 'by abortion monocotyledonous'. In *Allionia*, the next genus, the embryo is described as being plicate, the inner cotyledon being shorter than the outer.

Hildebrand has pointed out, by removing the lamina of the seed-leaf of the young seedling. A more certain way of stimulating the rudimentary second cotyledon to develop, however, is to remove not only the blade but also the greater part of the petiole of the original seed-leaf. The second cotyledon is also frequently stimulated to develop if by any chance the lamina of the first cotyledon should be unable to escape from the seed-coats and so fail to function as an assimilating organ.

The second cotyledon is, as a rule, a smaller organ than the first, but otherwise it is very similar in general appearance; the apical notch so characteristic of the seed-leaf is usually noticeable, and the margins tend to be smooth and are not as a rule provided with the serrations which are characteristic of the margins of the plumular leaves. Conspicuous surface markings, which are a feature of the plumular leaves of *Cyclamen*, are also absent from the laminae of both cotyledons.

The vascular structure of the cotyledonary petioles shows some difference from that of the petiole of the young plumular leaves, but the differences are not constant. In the plumular leaf-petioles, especially near the lamina, there is usually a definite reniform stele surrounded by a distinct pericycle and endodermis and enclosing some three to seven radiating xylem groups of equal size.

In both the cotyledonary petioles, however, the vascular structure, as Miss Sargent noted for the first cotyledon, suggests a double structure. The xylem elements are arranged in two well-developed lateral groups, especially near the base of the petiole, while near the apex a somewhat feeble median xylem group may be seen in cross-section. The double type of bundle, which to some extent seems to be associated with a slender petiole and a small lamina, has also been noticed in sections of the petioles of adventitious leaves arising from the decapitated tuber.¹

¹ Mr. Boodle has kindly examined sections of the petioles, and has made the following observations:

‘In the double bundle there are sometimes two protoxylem groups, one to each xylem mass, or sometimes there are three protoxylems, two to the larger group of xylem, one to the smaller. The latter case gives an indication of the triple structure attained higher in the petiole by division of the larger xylem group, accompanied by displacement whereby one of these groups takes up a median position.

‘Where the base of the petiole has a triple bundle there may be three protoxylems, but here,

TEXT-FIG. 2. *C. neapolitanum*. The cotyledonary lamina with the seed have been removed, and the second cotyledon, *c. 2*, is developing. The petiole of the normal cotyledon, *c. 1*, is beginning to wither.

TEXT-FIG. 3. *C. neapolitanum*. The first cotyledon, *c. 1*, has been unable to free its lamina from the seed-coat, and the second cotyledon, *c. 2*, has developed and expanded its lamina.

Passing now to the behaviour of the cotyledonary and plumular leaves when subjected to artificial mutilation, some striking differences are noticeable, as Winkler and Goebel¹ have pointed out.

If the lamina of the first cotyledon be removed, there will arise, from one or from both the ridges on the inner side of the petiole, just below the cut surface, small protuberances which will gradually develop into new laminae.

The new laminae grow out from the petiole as decurrent wing-like organs, and like the lamina are bifacial with their upper surfaces facing

FIG. 4.

FIG. 5.

FIG. 6.

FIG. 7.

TEXT-FIGS. 4-7. 4. *C. persicum*. The petiole of the normal cotyledon with the lamina removed. A new lamina, L. 2, has developed from the edge of the groove of the petiole near the cut surface. Back and front views. 5. *C. balearicum*. The formation of new laminae, L. 2, from the cotyledonary petiole. 6. *C. persicum*. The new lamina, L. 2, has developed a petiole and the lamina has been removed. 7. The development of new laminae, L. 3, from the secondary petiole.

inwards. These new laminae are thus in their position at right angles to the original lamina of the cotyledon. Sometimes they remain as longitudinal wings or flanges attached by a broad base to the upper part of the petiole, but more often they assume the form of small leaves and develop distinct petioles of their own.

If after a time the upper part of the original petiole with the new laminae be removed, the petiole will again produce new laminae just below the cut surface, and it has been found that even if as much as 6 mm. of the apical portion of the cotyledonary petiole be removed new laminae will be and also in double bundles, the protoxylems may be more or less united, so that an apparently single, rather diffuse, protoxylem group may occur on the adaxial side of the bundle.'

¹ Winkler: Ueber die Regeneration der Blattspreite bei einigen *Cyclamen*arten. Ber. d. Deut. Bot. Gesellsch., xx, 1902, p. 81.

Goebel: l. c., 1902, pp. 436-8, Figs. 10-13; and l. c., 1908, p. 203, Fig. 105.

Similar experiments were made by me at Cambridge in 1907 and 1908 on *Cyclamen balearicum* and *C. neapolitanum* independently of Winkler's and Goebel's work.

developed from the top of the decapitated petiole. Similarly, if one of the new lateral laminae be removed from its petiole, this secondary petiole is capable of producing a new lamina in the same way as does the main petiole of the cotyledon.

I have also been able to confirm Goebel's experiments with the hypocotyl of the *Cyclamen* seedling;¹ for if the top of the tuber with its plumule be removed, a series of adventitious leaves with petioles are formed round the periphery of the mutilated tuber from the cut surface (Pl. XX, Figs. 4 and 7, and Text-Fig. 8). The new leaves, in the cases which have been observed, arise with their outer or lower surfaces directed towards the centre of the tuber, and not, as figured by Goebel, with their inner or upper surfaces facing inwards. As they develop, however, they sometimes change their position and face the centre of the tuber. The decapitated upper portion of the tuber bearing the plumule will also send out adventitious roots from the cut surface—i.e. the lower surface—and behave as a true cutting.

The power of regeneration displayed by the hypocotyl is well known in some other plants, as for instance *Anagallis coerulea* and *Linaria cymbalaria*, in which, if the cotyledons and plumule be removed, new buds are formed freely on the hypocotyl.² A similar development of hypocotyledonary shoots also occurs in *Linum usitatissimum*, *Linaria bipartita*, and *Antirrhinum majus* on decapitation of the seedlings.³

The hypocotyl of *Cyclamen* appears to differ at first from the cases just mentioned, since for about a year laminae only are produced from the edge of the cut surface, and there are no signs of the formation of new growing-points from the tissues of the decapitated tubers. In the case of older tubers, as Goebel points out, adventitious shoots will also arise when the tubers are decapitated, but the new laminae and growing-points arise from the actual cut surface near the centre of the tuber instead of from the margin (Pl. XX, Fig. 6).

A further example of limited meristematic activity is shown by the cotyledon itself when that organ with its petiole is severed from the hypocotyl and treated as a 'cutting' (Pl. XX, Fig. 2).

In the course of a few days, under suitable conditions, roots are freely

TEXT-FIG. 8. A seedling of *C. persicum* from which the top of the tuberous hypocotyl with the cotyledon has been removed. Adventitious leaves arise from the tuber just below the cut surface. The specimen shows four rudimentary and the backs of two fully developed leaves.

¹ Goebel: l. c., 1902, pp. 482-4, Figs. 14, 15; and l. c., 1908, p. 204, Fig. 106.

² Küster: Beobachtungen über Regenerationerscheinungen an Pflanzen. Bot. Centralbl. Beihefte, xiv, 1903, p. 316.

³ Burns and Hedden: Conditions influencing Regeneration of Hypocotyl. Bot. Centralbl. Beihefte, xix, 1906, p. 383.

produced from the base of the petiole and grow vigorously, being supplied with carbohydrates by the green lamina.

These leaf-cuttings will live for months, both lamina and stalk increasing considerably in size, but though numerous experiments were made at various seasons, it appeared that the tissues had no power to develop a growing-point and in due course the rooted leaf died.

A series of *Cyclamen* cotyledons were, however, put in as cuttings in October, 1918, in order to see whether any further stages in development would take place, and somewhat unexpected results were obtained. The petioles produced roots from the base readily as before, and in the following February (1919) a second leaf was found to be developing. On examination it was seen that a small tuber had formed at the base of the petiole as a lateral outgrowth, and it was from this tuber that the second leaf, which was plumular in character, had arisen. Nearly all the leaf cuttings put in at this time behaved in this manner (Pl. XX, Fig. 3, and Text-Figs. 9, 9a).

The tuber increased in size and produced roots from near the upper surface by the side of the cotyledonary petiole. Roots were not produced from the lower surface of the tuber, so that the corm was considerably different in character from the corm of a normal seedling, being smooth and rounded below and having a tuft of roots on one side only, close to the developing plumule.

The young plants developed adventitiously from the cotyledon have continued to grow and produced a plumule with several leaves and flowers (March, 1920).¹

So far the regenerative capacity of the first cotyledon only has been referred to; it is of interest, therefore, to examine the behaviour of the plumular leaves under exactly similar conditions of treatment.

If the lamina of the first, or of any subsequent, plumular leaf be removed, no new lamina is developed from the petiole, and in the course of a few days the petiole withers and dies.

Further, such plumular leaves with their petioles were treated as 'cuttings', as described for the cotyledons, but after repeated experiments

¹ The behaviour of the leaves of the ivy-leaved *Pelargonium* when treated as cuttings was brought to the notice of the Scientific Committee of the Royal Horticultural Society, so Mr. Chittenden informs me, by Mr. Houston on October 15, 1901. As is the case with the cotyledon of *Cyclamen*, roots were freely produced from the petiole, but no buds developed. I have found, however, in the case of leaf cuttings of *Tricuspidaria lanceolata* that both roots and a shoot are produced from the base of the petiole. Ivy leaves put in as cuttings will produce leaves but no shoots, and have lived in this condition for five years, and leaves of *Hoya* in like manner for seven years (Carrière-Jardinier, *Multiplicateur*, s. 218). De Vries (Prings. Jahrb., xxii, 1891, pp. 68-70) refers to similar rooted leaf cuttings of *Aucuba*, *Euonymus japonicus*, *Ficus elastica*, and *Camellia japonica*, which appear to be incapable of developing adventitious buds and forming plants from leaf cuttings. He quotes from Mer (Bull. Soc. Bot. France, xxvi, p. 26), who refers to the case of the ivy-leaf cuttings.

In the Gardeners' Chronicle, Feb. 15, 1845, p. 101, D. Beaton refers to the formation of 'callosities' on the petioles of leaves treated as cuttings, and to the formation of buds in some cases; in others, as *Camellia*, the leaves lived for four years without the formation of buds.

there was no production of adventitious roots from the base of the petiole as with the cotyledon. The base of the petiole, however, enlarged considerably and formed a kind of tuber or callosity, but, though shaving of the surface of this callosity and other devices to induce root formation have been tried, the results have only been negative. The leaf cutting may remain alive for a considerable time and increase in size, but it will eventually

TEXT-FIG. 9. *C. persicum*. A first cotyledon cutting more fully developed (cf. Pl. XX, Figs. 2, 3), showing the cotyledon, *c.*, and plumular leaves, *pl. 1* and *2*. The adventitious tuber shows two growing-points, *gp 1*, *gp 2*. The root is developed from the upper surface or, more correctly, the tube is developed below the root, and is more clearly seen in the back view, 9 *a*.

die without having formed either root or shoot. One exception to this statement, however, must be recorded, as in one case only a young plumular leaf from a young seedling did develop a root from the base of the petiole, and the leaf cutting, which developed a strong laterally placed root, remained alive until February, 1920; there was, however, no development of an adventitious bud (Pl. XX, Fig. 1, and Text-fig. 10).

A section through the callosity or swollen base of the petiole reveals several cortical 'nests' of lignified cells—and a few such 'nests' are also

seen at the base of the cotyledonary petiole—but for some unknown reason, except in the single case mentioned, the cells of the plumular leaf appear to be unable to produce any adventitious outgrowths in the way of roots.

To return now to the second cotyledon of the *Cyclamen* seedling. It has been shown that the normal single cotyledon shows marked differences from the plumular leaves when mutilated by removal of the lamina which affords a certain means of distinguishing the two organs. It becomes therefore a matter of interest to examine the behaviour of the second cotyledon under like conditions, more especially as additional evidence may thus be obtainable in support of the contention that the embryo of *Cyclamen* is truly dicotyledonous.

From a number of seedlings in which the second cotyledon had been induced to develop, the laminae were removed, and in due course the response was exactly comparable to the traumatic reaction obtained with the first cotyledon, though, owing to the less robust character of the petiole, the percentage of successes was considerably smaller. From the apex of the petiole an outgrowth arises either on one or on both sides of the groove of its inner surface and develops to form a new assimilating organ as a flange or wing-like organ placed at right angles to the original lamina (Pl. XX, Fig. 5, and Text-figs. 11, 12).

Leaf cuttings of the second cotyledon have also been made and in the majority of cases roots have developed from the base of the petiole exactly as occurs with the first cotyledon; such rooted cuttings have not, however, produced adventitious buds or developed a plumule. As in the case of the first cotyledon there was no formation of a callosity at the base of the petiole (Text-fig. 13).

The leaves produced from the edges of the decapitated seedling tubers, being, as it may be assumed, 'cotyledonary' in character, were next tested to see whether they would respond to wounding in the same manner as do the first and second cotyledons, and it was of considerable interest to find that their response was quite similar. When put in as cuttings, roots were developed quickly from the base without a swelling being formed, but no formation of adventitious buds has so far been observed (Text-fig. 14). It may be that both with these adventitious leaves and with the second cotyledons adventitious buds might be formed if conditions should happen to be favourable.

The laminae of these adventitiously produced leaves were also removed, and a new lamina was developed from the edge of the petiole near the apex, in precisely the same manner as new laminae are produced from the petioles of the mutilated cotyledons (Text-fig. 15).

These experiments are of interest, since they tend to show that the adventitious leaves produced from the edge of the cut surface of the

FIG. 10.

FIG. 11.

FIG. 12.

FIG. 13.

FIG. 14.

FIG. 15.

TEXT-FIGS. 10-15. *C. persicum*. 10. A first plumular leaf put in as a cutting Nov. 6, 1918, which developed a callus and also roots—the drawing was made March 21, 1919. The cutting died nearly a year later. 11. A seedling in which the second cotyledon, *c. 2*, has been produced on removal of the first cotyledon (scar, *c. 1*). The lamina has been removed, and flange-like laminae, *l. 2*, have developed from the edges of the groove on the adaxial surface of the petiole. The first plumular leaf, *p. 1*, has grown up. 12. One of the flange laminae of the second cotyledon in side view. 13. A second cotyledon struck as a 'cutting'. As with the first cotyledon, there is no swelling at the base of the petiole. 14. An adventitious leaf developed from a decapitated seedling tuber (see Pl. XX, Fig. 4, and Text-fig. 15) struck as a cutting. The roots are formed as in the cotyledon cuttings, and there is no swelling at the base of the petiole. 15. A tuber of a seedling *Cyclamen* from which the upper portion has been removed, showing one fully developed adventitious leaf and others as marginal protuberances. The lamina of the leaf was removed, and a new lamina, *l. 2*, has developed from the surface of the petiole exactly as occurs when the lamina of a cotyledon is removed.

decapitated hypocotyledonary tuber are still in the 'embryonic' condition and are comparable both physiologically and morphologically to the cotyledons.

Older tubers which had given rise to plumular leaves were also decapitated for comparison with the seedling tubers, but it was found that in such cases the adventitious leaves were produced not from the edges of the cut tubers, but from the cut surface itself close to the centre of the tuber (Pl. XX, Fig. 6). These leaves were plumular in appearance, and were found to behave as do the normally produced plumular leaves. New laminae could not be produced from the petioles when the original laminae were removed, nor could the leaves be induced to form roots when treated as 'leaf cuttings', though they formed a callus in the same manner as do the plumular leaves.

In both the decapitated seedling and adult tubers one or more plumular buds will develop in course of time and apparently normal *Cyclamen* plants result. The tubers become rounded above by the growth of the tissues of the tuber which are protected by corky tissue. They differ, however, in most of the cases examined in having several plumular shoots instead of the single axis developed by normal plants (Pl. XX, Fig. 7).

SUMMARY.

Arguments have been brought forward on morphological grounds to show that the rudimentary curved body lying opposite the cotyledon proper in the *Cyclamen* embryo is the second cotyledon, and that under ordinary conditions it does not develop to form a green leaf.

When artificially induced to develop, however, it is found to respond to the traumatic stimulus of the removal of the lamina by regenerating a new lamina or laminae from the petiole, exactly as does the normally developed first cotyledon.

The evidence afforded by this power of regeneration may therefore be accepted as definite proof that the embryonic rudiment is undoubtedly the undeveloped second cotyledon.

The *Cyclamen* seedling, though aberrant in type, is thus seen to be truly dicotyledonous in nature.

Thus, though the second cotyledon of *Cyclamen* has ceased to function as an absorbent organ in the seed, possibly in correlation with the geophilous habit of the genus, it is of interest to find that, when stimulated to develop as an assimilating organ, it is in the physiological state characteristic of and peculiar to the cotyledon proper—a condition which is not shared by any of the plumular leaves which arise subsequently from the shoot.

It has also been found that the leaves adventitiously developed from the edge of decapitated seedling tubers—the swollen hypocotyl—respond to traumatic stimuli in precisely the same manner as do the cotyledons.

EXPLANATION OF PLATE XX.

Illustrating A. W. Hill's paper on Studies in Seed Germination.

The photographs have kindly been taken by Mr. J. Hutchinson, The Herbarium, Kew.

All the specimens figured in the plate are *Cyclamen persicum*.

Fig. 1. *Cyclamen*. A young plumular leaf put in as a cutting. A callus has developed, but no roots have been formed; the leaf lived in this condition for about a year.

Fig. 2. *C*. A cotyledon—the normally produced first cotyledon—put in as a cutting. Roots are quickly developed from the base, and there is no formation of a knob of callous tissue.

Fig. 3. *C*. A cotyledon cutting, showing a further stage of development. A tuberous swelling has grown out at the base of the root, and on this a plumular bud has formed which has given rise to plumular leaves and shoots; the lower side of the tuber is rounded and the roots are produced from the upper surface.

Fig. 4. *C*. A decapitated seedling tuber, showing the development of adventitious leaves from the surface of the tuber just below the cut surface. The adventitious leaves behave exactly as do the cotyledons.

Fig. 5. *C*. Two seedlings, from which the first cotyledon has been removed. The scar, *c. 1*, can be seen. The second cotyledon, *c. 2*, has developed, and the lamina has been removed. In each case new laminae have developed from the adaxial side of the petiole.

Fig. 6. *C*. An older tuber decapitated. In this case several plumular leaves had developed before the upper half of the tuber was removed. New adventitious plumular buds have been formed from the centre of the cut surface of the tuber, and not from just below the margin of the cut as in the seedling. The adventitious leaves in the case of these adult tubers behave as do the plumular leaves.

Fig. 7. *C*. A decapitated seedling tuber, about a year old, which has developed two plumular axes from the margin. The surface of the cut can still be distinguished.

Hill, Arthur William. 1920. "Studies in seed germination. Experiments with Cyclamen." *Annals of botany* 34, 417-429.

<https://doi.org/10.1093/aob/os-34.4.417>.

View This Item Online: <https://www.biodiversitylibrary.org/item/236972>

DOI: <https://doi.org/10.1093/aob/os-34.4.417>

Permalink: <https://www.biodiversitylibrary.org/partpdf/320298>

Holding Institution

Smithsonian Libraries

Sponsored by

Biodiversity Heritage Library

Copyright & Reuse

Copyright Status: Not in copyright. The BHL knows of no copyright restrictions on this item.

This document was created from content at the **Biodiversity Heritage Library**, the world's largest open access digital library for biodiversity literature and archives. Visit BHL at <https://www.biodiversitylibrary.org>.