

SPIRODISTICHY RE-INTERPRETED

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[Plate 1]

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The chief peculiarity of spirodistichous phyllotaxis, shown, for example, by *Rhoeo discolor*, is that it is spiral instead of distichous, although each leaf makes contact at its base with the next older leaf only. Previously (1951) the writer suggested as an explanation that in this species the position of each new leaf depends on a balance of physiological repulsions from the centres of the two or more next older leaves; for it did not seem possible to explain the spirodistichy on the basis of a space-occupying theory such as had been found to hold good for various dicotyledons. This suggestion was based on experiments in which the central part of P_1 , the youngest visible leaf, was removed, and the angular positions of the subsequent leaves, I_1 and I_2 , were found to differ from the normal in such a way that these leaves appeared to be displaced towards the removed leaf centre. But later it was found that when the central part of P_2 was removed, I_1 was not appreciably displaced towards P_2 , as it was expected to be, unless the part removed was very large. This made the previous explanation very doubtful, and another explanation was sought. It was found by measurements of the angles between older leaves that the growing-point of the apex shifted away from the wound after the operations on P_1 , but only after the more severe of the operations on P_2 . It is shown that on the basis of a space-filling theory of leaf determination the shift of the growing-point, acting in various ways, is enough to account for the displacements of I_1 and I_2 towards the wound after the previous operations on P_1 and the displacement of I_1 after the more severe operations on P_2 .

The question arises therefore whether the normal spirodistichy can be explained without postulating physiological repulsions. It is shown that in *Rhoeo* the flanks of a leaf, extending round the apex, are able to approach the summit of the apex in passing over an obstacle, and it is suggested that the phyllotaxis is spiral because each new leaf, n , is caused to deviate laterally by the flank of leaf $n-1$ beneath it, which rises towards the summit of the apex in passing over the centre and axillary bud of leaf $n-2$, a suggestion first made to the writer by Professor G. van Iterson. Also the results of other operations on the apex of *Rhoeo* are reported and are interpreted similarly on the basis of a space-filling theory, as due to the shift of the growing-point acting in various ways, and the peculiar powers of development of the leaf flanks. The development of the axillary buds and seedlings is described and interpreted on a similar basis. So it is not necessary

to postulate physiological repulsions in order to explain leaf determination in *Rhoeo*, nor to suppose that the process is fundamentally different from what it is in dicotyledons.

The base of each leaf in *Rhoeo* is normally asymmetric, its anodic half being shorter peripherally, but thicker radially. After various operations on the apex the shapes of the bases of the next three leaves that arise are often changed, and a study of these changes has made it possible to suggest an explanation of the asymmetries of the leaves both after the operations and in normal apices. Some changes in the eccentricities of axillary buds are also reported.

1. INTRODUCTION

In a previous paper the writer (1951) discussed the spirodistichous phyllotaxis found in many monocotyledons, and reported a study of it in *Rhoeo discolor*. It was studied both by detailed observations of the normal shoot apex of *Rhoeo* and by experiments, and it was concluded that the position in which each new leaf was determined in that species depended mainly on a balance between physiological inhibitions or repulsions coming from the central parts of the two previous leaves. The still older leaves were thought to inhibit more feebly. Thus the process of leaf determination seemed to be quite different from what it was in dicotyledons, in which it had been concluded that each new leaf occupies in turn the lowest sufficient space on the apical cone (Snow & Snow 1931, 1933, 1935, 1947, 1952), and that in *Lupinus albus* at least the existing leaves do not repel the new leaf (Snow & Snow 1952, p. 562).

One reason for this conclusion was that in the normal apex of *Rhoeo* the morphological centre of a new leaf does not come quite in the slight depression above the junction of the edges of the previous leaf, which was thought to be the lowest part of the apical cone (see figure 1). Another reason was that when the central part of P_1 , the youngest existing leaf, was removed, then I_1 and I_2 , the first two leaves that arose after the operation, were displaced towards the normal position of the centre of P_1 , and away from the centre of P_2 . Yet they did not appear to be moving into lower positions on the apical cone, and, moreover, I_2 does not even make contact with P_1 at its base, but only with I_1 , since each leaf encircles the apex. So it seemed that normally in this species the position of a new leaf depended partly on some influence coming from the second older leaf, as well as from the next older, and that this influence must be physiological and not due to occupation of space on the apex, since the second older leaf does not touch the new leaf at its base (Snow, M. 1951, p. 157). The results of this operation in ten apices were recorded in tables 2 and 3 of the previous paper.

But if the position of a new leaf in *Rhoeo* depended on a balance of repulsions coming mainly from the central parts of the two previous leaves, then I_1 would be displaced the other way if the central part of P_2 instead of P_1 were to be removed. A few such experiments had indeed been done when the previous paper was written, though they were not mentioned; and some of them had shown a slight shift of I_1 in the expected direction. But in a subsequent series of these operations on P_2 , often I_1 did not shift appreciably, and it began to appear that I_1 shifted only when the removed piece of P_2 was specially large. This result, together with some other results and observations, led the writer to doubt the previous interpretation, and soon afterwards Professor G. van Iterson suggested in a letter a way in which the normal phyllotaxis of *Rhoeo* might be explained without postulating physiological repulsions. So it became necessary to reconsider the whole question and to

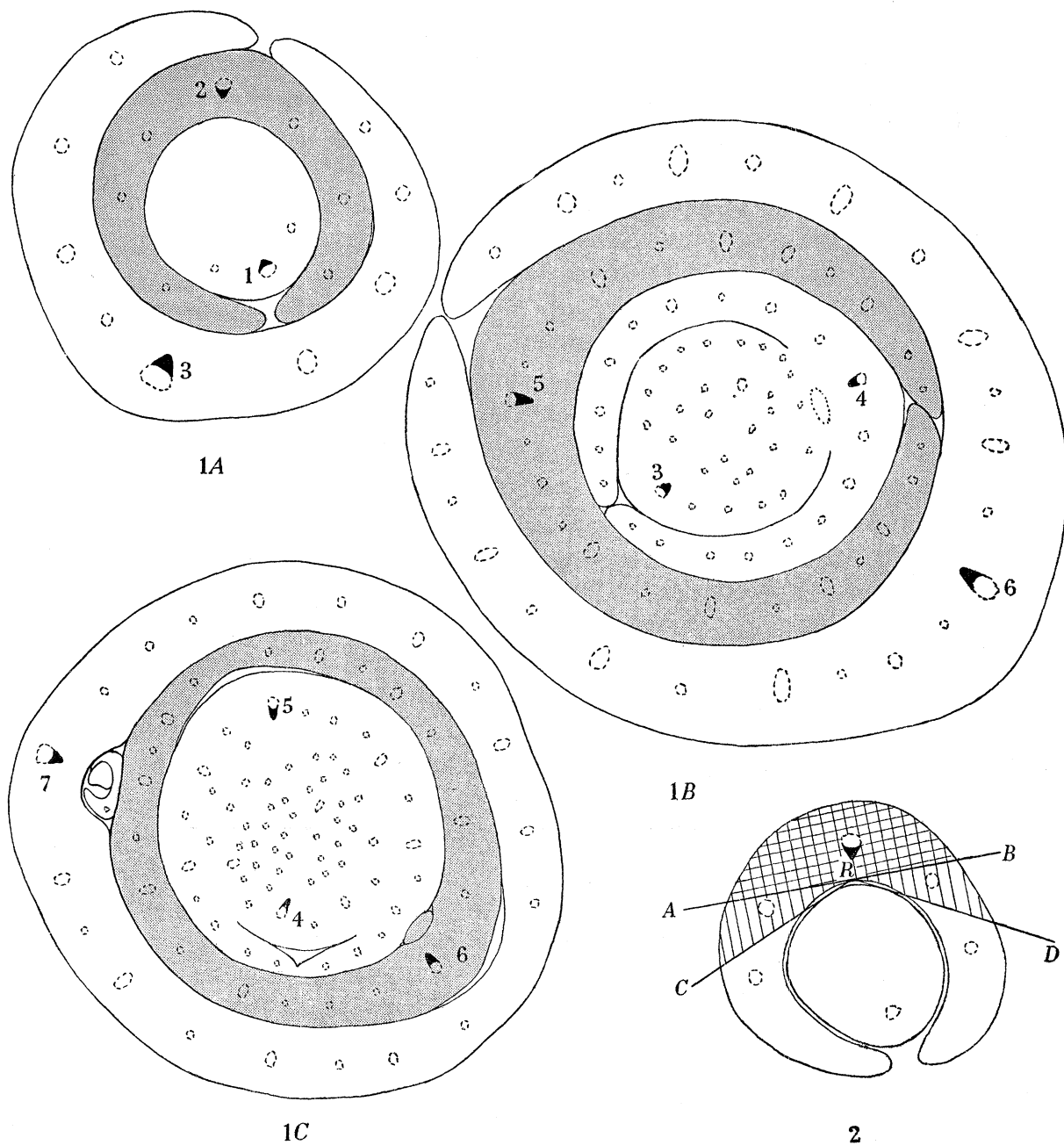


FIGURE 1. *A* and *B* are transections of a normal apical bud of *Rhoeo discolor*, and *C* is a transection of another such bud at a lower level. In this and subsequent figures the leaves with their axillary buds are shown alternately clear and stippled to guide the eye; conducting and desmogen strands are outlined with broken lines and the cells with dense contents immediately beneath an axillary bud are enclosed within a dotted line. The xylem regions of the median vascular strands are shown black. (Magn. *A*, $\times 75$; *B*, $\times 37$; *C*, $\times 20$.)

FIGURE 2. Diagram to show the parts of the central region of P_2 that were removed, as seen in transverse section. In all apices the central part of P_2 delimited by the line *AB* and cross-hatched was removed, and in some apices the parts of the flanks shown with line shading were also removed.

investigate it further. In the present paper, therefore, the results of removing the centre of P_2 will be reported, and then there will be suggested a new interpretation, not involving physiological repulsions, for the displacement of I_1 after the previous operations on P_1 , and also for its position after the similar operations on P_2 . Next the new suggestion concerning the normal phyllotaxis of *Rhoeo* will be discussed, with some relevant observations. Then the subsequent changes after the removal of the centre of P_1 will be discussed, and the results of some operations of other kinds will be reported, which serve to test the new suggestion. Lastly, the development of the phyllotaxis in axillary buds and seedlings and the asymmetries of the leaves will be described and discussed. The methods were the same as before (1951), the apices being operated upon free-hand under a binocular at magnification of $\times 75$, and pickled for sectioning usually after about 6 weeks, which are equivalent to 4 to 5 plastochrons. All the apices were embedded in collodion except those of the young normal seedlings which were embedded in paraffin.

2. THE POSITION OF I_1 AFTER REMOVAL OF THE CENTRAL PART OF P_1 OR P_2 , AND THE SHIFT OF THE GROWING-POINT

The results of twenty operations in which the central parts of the P_2 's were removed by cuts are given in table 1. The cuts were made obliquely downwards and outwards, being intended to shave off the central part of the leaf right down to its base, and not to penetrate

TABLE 1. TWENTY APICES IN WHICH THE CENTRAL PART OF P_2 WAS REMOVED

numbers of apices	size of P_1 when operated	All measurements in degrees.					arcs of anodic halves of leaves			strand number ratio a/k of P_1 (normal 0.82)
		divergence angles					P_1 (normal 166.5)	I_1	I_2	
		P_4-P_3 (normal 152.6)	P_3-P_1 (normal 54.8)	P_1-I_1	I_1-I_2	I_2-I_3				
first series										
130	medium	—	56	150	150	149	—	166	—	—
136	very small	149	54	157	143	157	166	160	—	0.92
129	small medium	160	62	158	143	158	170	159	—	1.00
131	very small	—	—	161	148	150	175	168	—	1.08
266	very small	157	58	161	143	158	171	160	169	0.92
133	very small	—	—	168	139	—	177	166	—	0.73
132	very small	162	72	180	132	162	180	158	180	1.08
second series										
178	very small	—	59	152	156	147	180	159	159	0.92
159	very small	162	57	153	148	155	167	167	170	0.93
149	very small	155	62	154	157	150	167	165	168	0.92
146	very small	154	60	155	149	149	171	163	165	1.0
148	very small	152	53	156	148	156	162	163	167	0.93
156	very small	156	50	156	149	155	170	166	165	0.73
144	very small	159	62	158	142	148	175	165	164	—
third series										
229	very small	155	58	159	140	158	173	157	175	1.09
235	small medium	—	—	160	152	153	171	161	169	0.91
220	very small	156	57	162	143	159	172	161	173	1.18
224	very small	—	56	165	147	156	178	160	179	0.92
234	very small	—	—	165	147	150	177	173	169	1.11
228	small	166	71	177	136	160	187	159	173	1.0

the axis below it; but this may not always have succeeded exactly. The horizontal extents of the parts removed varied, and are indicated in figure 2, which is a section of a normal apex with the cuts as seen at the time of operation. Sometimes only the part of P_2 outside the line ARB was removed, but sometimes the triangular regions ARC and BRD were removed also, so that the operations were then more severe.

In the apices first operated upon, which are recorded in series 1 of table 1, it was found that the angle P_1-I_1 was not much increased except in the last two apices of this group, nos. 133 and 132. Subsequently the apices were intentionally operated upon either in a less severe or a more severe manner, the two kinds of operation being roughly such as are shown in figure 2. The less severe operations, of which an example, no. 159, is shown in figure 3, are the seven included in series 2 of table 1, and after none of these did the angle P_1-I_1 significantly exceed the normal mean value of 152.6° . The greatest increase was only 5.4° , and the mean increase 2.3° , whereas the standard deviation of a normal divergence angle was found previously to be 3.7° , and that of the normal mean to be 0.42° (Snow, M. 1951).

But in the six apices of series 3, which were operated upon in the more severe manner, the increases of P_1-I_1 ranged from 6.4° to 12.4° , apart from one outstanding increase of 24.4° in no. 228; and some of these increases are significant. An example, no. 224, is shown in figure 4.

These results are inconsistent with the previous theory of physiological repulsions. For on that theory, as already pointed out, the angle P_1-I_1 would be expected always to increase when the central part of P_2 was removed, I_1 being repelled by P_1 . But now this angle has been found not to increase significantly after removal of a fairly large central part of P_2 , a part relatively quite as large as the central part of P_1 of which the removal did previously displace I_1 the other way (Snow, M. 1951). It therefore needs to be considered whether it is possible to explain otherwise than on a theory of physiological repulsions the displacements of I_1 towards the removed centre of P_1 found previously, and also its displacement towards P_2 in the most severe group of removals of the central part of P_2 .

It has regularly been found in *Lupinus albus* and other dicotyledons that cuts made in one side of the apical cone displace the extreme summit or growing-point away from the wound (Snow & Snow 1931, pp. 6, 7). Even the operation of isolating P_1 by a vertical cut descending into the axis below its insertion did this, though less strongly. The shift of the growing-point was regularly followed by changes in the angles between the leaves formed soon after the operation such that the leaves seemed to be displaced towards the wound. Their displacements were partly apparent, due to changes of the centre from which the angles were measured, and partly real, as was shown by the positions of these leaves in relation to the leaves below; and the real part of the displacement was interpreted as due to the increase of available space on the apex above the wound. (By a real displacement of a leaf it is not, of course, meant that a leaf is first formed and then moved, but only that it is formed in an abnormal position in relation to the leaves below it.)

In the experiments on *Rhoeo*, however, it was not at first thought that the growing-point had shifted, since it had not done so conspicuously. But this may have been due to the flatness and asymmetry of the *Rhoeo* apex, of which a longitudinal section is shown in

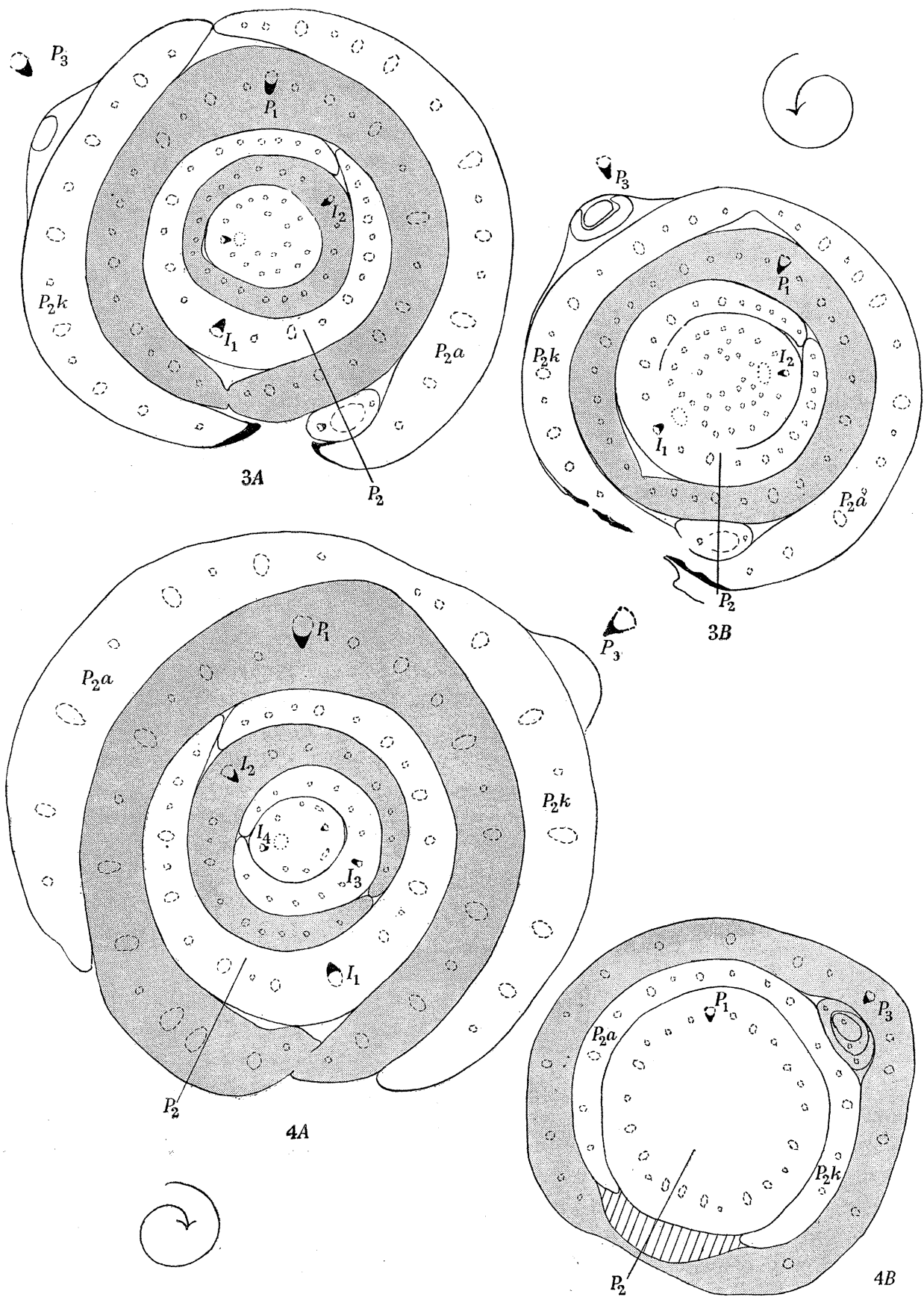


FIGURE 3. *A* and *B* are transections of apex no. 159 from above downwards. The centre of P_2 was removed. In *B*, P_2 is joined to P_3 in the region of the wound. In this and subsequent figures the small spiral indicates the direction of the genetic spiral. The shaded areas indicate the regions damaged by the wound and the heavy black lines indicate wound scars. Where a leaf centre has been removed its approximate angular position is indicated by a straight line or an arrow and its anodic and cathodic flanks are marked *a* and *k* respectively. (Magn. *A*, $\times 25$; *B*, $\times 20$.)

FIGURE 4. *A* and *B* are transections of apex no. 224 from above downwards. The centre of P_2 was removed. (Magn. *A*, $\times 34$; *B*, $\times 16$.)

figure 5, since this makes it more difficult to locate the growing-point exactly. So it now seemed necessary to look into the question more closely.

For this purpose the angles P_3-P_2 and P_4-P_3 were measured in sections made at about the level of insertion of I_1 in five of the apices from which the central part of P_1 had been removed. In the sections of the other apices besides these five the necessary leaves from P_4 to P_2 were lacking or damaged. Since these leaves were present before the operation, the true angles between them may be assumed to have been within the normal range. But when the angles are measured in sections made above the insertion of P_1 , they will appear to be different if the growing-point has shifted, since the centre from which they are measured will be different. Thus a shift of the growing-point away from the wound will increase the angle P_2-P_3 and decrease P_3-P_4 , as can be seen in figure 6.

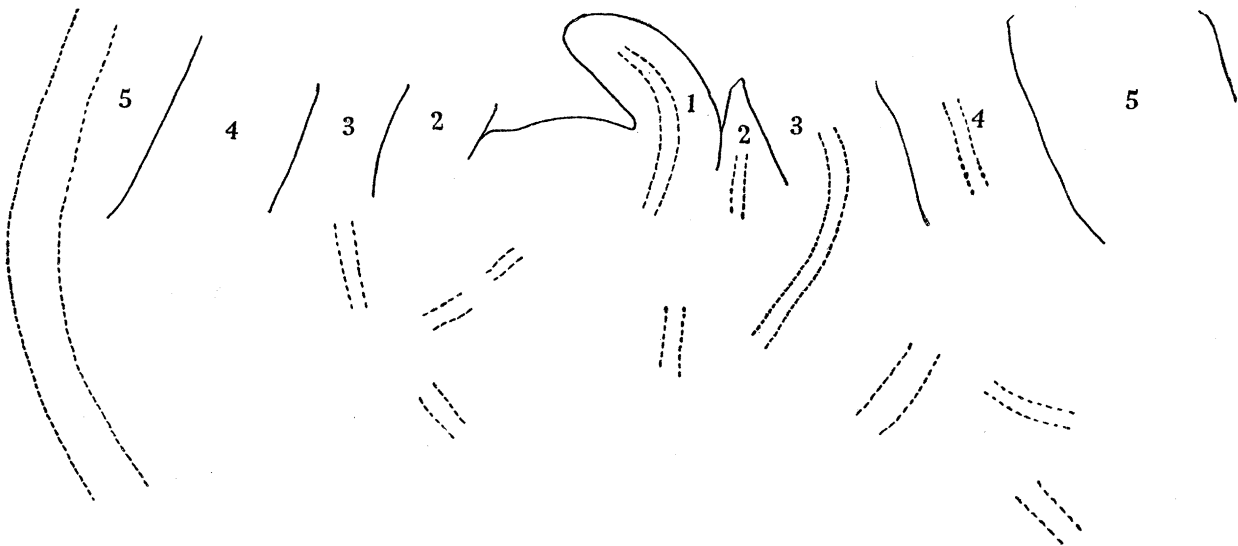


FIGURE 5. Longisection of a normal apex through the median plane of leaf 1. The leaves are numbered in order of age and, except for leaf 1, only their bases are shown. (Magn. $\times 86$.)

Actually it was found that the angle P_3-P_2 measured at this level in these five apices, nos. 5, 6, 7 and 8 of the previous paper and in one similar apex, no. 265 not previously reported*, exceeded the normal mean by 6.5° , 11.5° , 6.5° , 22.0° and 5.5° , while the angle P_4-P_3 was less than the normal by 10.5° , 6.5° , 12.5° , 12.5° and 2.5° . These measurements vary greatly, as can be understood, since there were many possible sources of error. But the changes are all in the same direction for each of the two angles, and they are strong evidence that the growing-point did indeed shift away from the wound when the centre of P_1 was removed. This shift would also decrease the angle P_1-I_1 , as is clear from figure 6, even if I_1 arose in its normal position in relation to P_1 ; and consequently it would contribute towards explaining the decrease of the angle P_1-I_1 (calculated from the angle P_2-I_1), reported previously. But in some at least of these apices the shift of the growing-point seems not to have been enough to account completely for the decrease of the angle P_1-I_1 ,

* In no. 265, figure 9, with central part of P_1 removed, the following angles were recorded: P_2-I_2 , 70.5° ; I_1-I_2 , 182.5° ; I_2-I_3 , 125.5° ; I_3-I_4 , 165° . I_1 and I_2 were thus displaced towards P_1 as in the previous apices and I_3 was in the smaller angle between I_1 and I_2 , as in nos. 3, 7 and 8 previously, so that the spiral returned to the original direction after I_2 . P_1 was rather small at the time of the operation.

and on a space-filling theory a real displacement of I_1 towards P_1 would also be expected as will be explained below.

When the centre of P_2 is removed, the angles from that centre cannot of course be measured, but a shift of the growing-point away from the wound would increase both the angles P_4-P_3 and P_3-P_1 if measured above the insertion of P_1 , as can be seen in figure 6. Table 1 shows that actually both these angles did increase in all three series of this experiment, and that the increase was much greater after the more severe operations of the third series, which also increased the angle P_1-I_1 considerably, than after the less severe operations of the second group, which increased P_1-I_1 only very slightly. So in

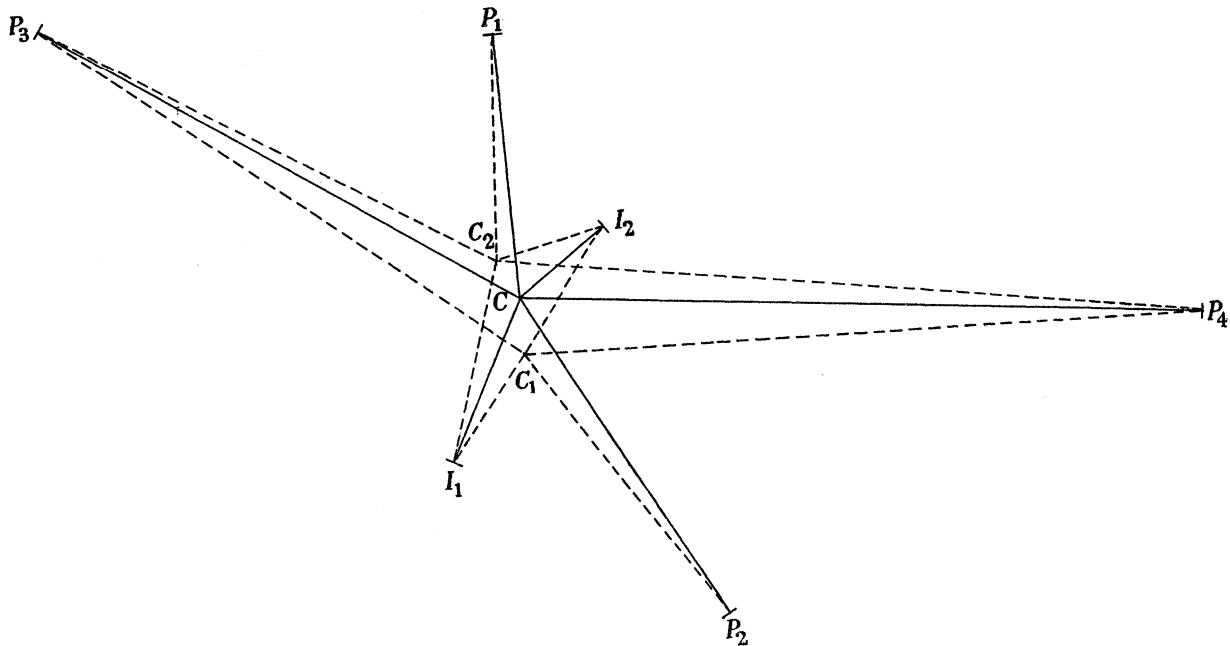


FIGURE 6. Diagram to show how the divergence angles between various leaves change when the growing-point shifts away from the removed centre of P_1 or P_2 . The points P_4 , P_3 , etc., mark the positions of the centres of these leaves. C is the original position of the growing-point, C_1 its estimated position after removal of the centre of P_1 , and C_2 its position after removal of the centre of P_2 . The angles between the radii from C to successive leaf centres are equal to the mean normal divergence angle. The ratios between the distances from C to the centres of successive leaves, called by Richards (1948, 1951) the plastochron ratios, are based on measurements of normal apices in the way explained in the appendix.

this experiment also there is good evidence that the growing-point did shift away from the wound, though after the less severe operations only very slightly, and these shifts of the growing-point must have accounted in part at least for such increases of the angles P_1-I_1 as were found. They appear indeed, from an estimate based on figure 6, to have been enough to account completely for the increases of this angle, but there may have been considerable errors in measuring angles from the old leaves P_4 and P_3 , which were cut down in preparing for the operation and may have grown unevenly. So it remains possible that another factor may have contributed to the increase of P_1-I_1 in this experiment, namely, a change in the shape of P_1 , which will be discussed in §4.

In order to understand the changes that took place in the apex immediately after the operation, several apices from which the centre of P_1 had been removed were examined

in the solid from above at intervals during the two following weeks. Figures 7*A*, *B* and *C* show three of these apices after 12, 6 and 14 days. The three apices differ in the state of development of I_1 ; in *A*, no. 264, I_1 has not yet arisen; in *B*, no. 273, I_1 has just arisen and subtends about 180° ; in *C*, no. 265, I_1 has encircled the apex. They differ also in the

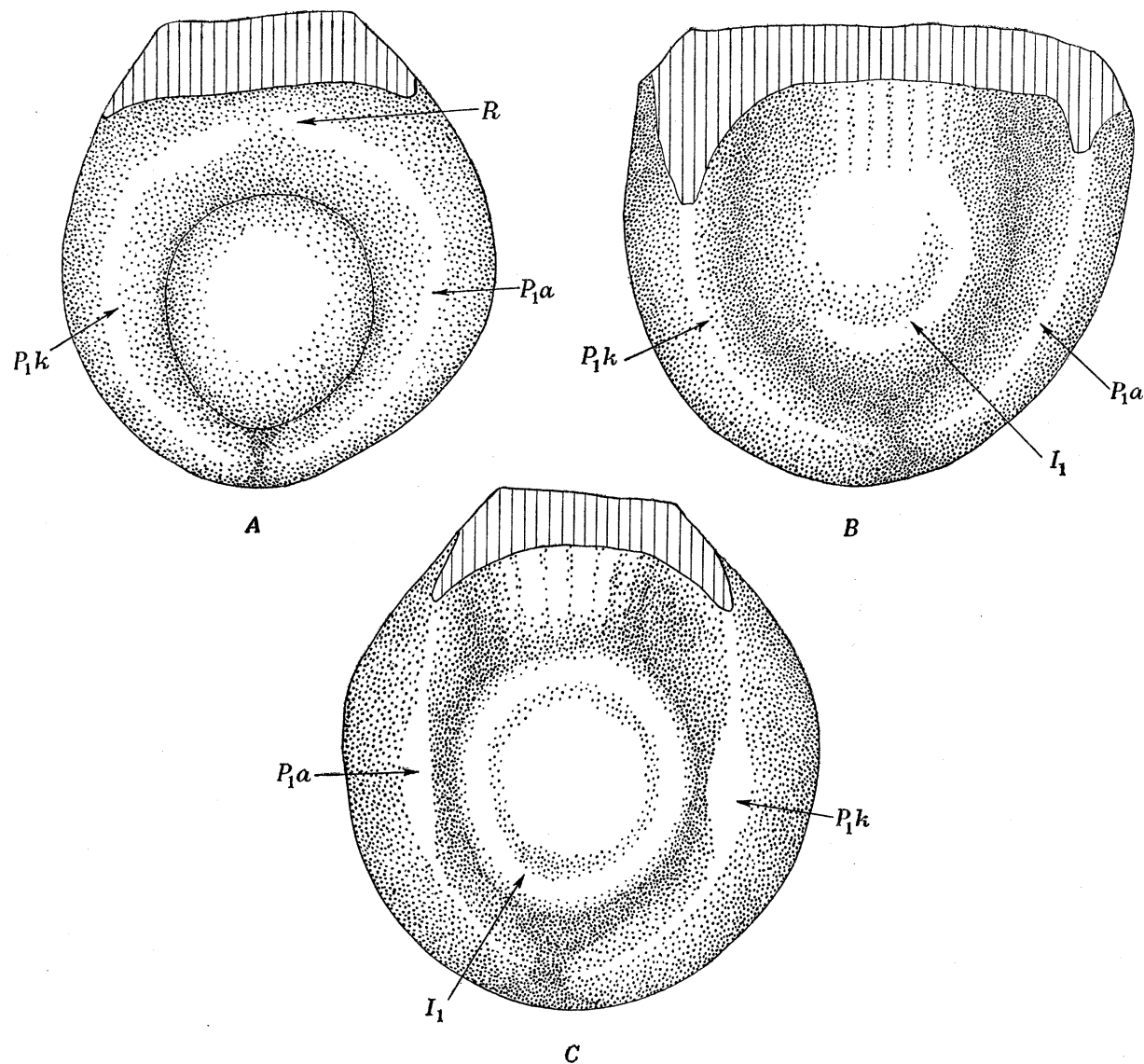


FIGURE 7. *A*, *B* and *C* are free-hand drawings of three apices from which the centre of P_1 had been removed. The light came from above. Horizontal and slightly oblique surfaces are illuminated; surfaces approaching the vertical are shaded with dots. Wound surfaces are indicated with line shading. P_{1a} and P_{1k} are the anodic and cathodic flanks of P_1 . *A*, apex no. 264, 12 days after operation. *B*, apex no. 273, 6 days after operation. *C*, apex no. 265, 14 days after operation. In *A* and *B* the spiral runs clockwise, in *C* counter clockwise. See text for further description.

manner of development of P_1 . In *A* the cut edges of the flanks of P_1 have grown towards each other and united above the wound at R . In *B* and *C* the flanks of P_1 have not reunited and were not seen to do so during the subsequent development of these apices. In *B* and *C* the development of the part of the apex abutting on the wound can clearly be

seen. In both the apex has broadened transversely in the median plane bisecting the wound, and the region above the wound is marked by radial rows of cells suggesting that the broadening was due to radial growth in this region. This radial growth must be responsible at least in part for the shift of the growing-point away from the wound and may also provide additional space for leaf formation above the wound.

In figure 7*B*, I_1 has not yet invaded the region of radial extension, but in *C* the cathodic flank of I_1 has arisen above this region and has probably occupied part of it. The apical cone is not circular but is extended in the median plane bisecting the wound, suggesting that radial growth has continued within the cathodic flank of I_1 . A later stage of development of *B* showed an enlarged cathodic flank of I_1 which appeared to have occupied part of the region of radial extension.

These observations provide evidence of the manner in which the cathodic flank of I_1 became radially thicker, as will be described in §4, through the increased radial growth of the region from which this flank arose. They do not, however, show conclusively whether or not the central part of I_1 was displaced towards the wound, since the position of its centre could not be exactly located when seen in the solid.

In *A*, which developed very differently, the reuniting zone of the flanks of P_1 has occupied most of the region of radial extension, though it is probable that there has also been some radial growth between the reuniting zone and the growing-point, since the apex has broadened in this region.

It is clear that in *C* a considerable part of the region of radial extension remained unoccupied. It cannot be said with certainty why this happened, but the evidence so far as available suggests that unless the region above the wound is occupied within 7 days of the operation it cannot be occupied at all, presumably because the tissues are then too old for leaf formation. The reuniting zone of P_1 , when it developed, was seen in three apices to have occupied the region adjacent to the wound by 6 or 7 days after the operation; but in the two experiments shown in figures 7*B* and *C* in which a reuniting zone of P_1 did not develop, the cathodic flank of I_1 did not reach this region until 9 and 11 days respectively after the operation. I_1 may thus have arisen too late to occupy the parts closest to the wound, but the reuniting zone of the flanks of P_1 arises earlier if at all, and is certainly able to do so. The apex shown in figure 7*C*, no. 265, was grown on afterwards and its divergence angles were recorded on p. 51 (footnote).

The above observations show that the shift of the growing-point after this operation is due at least partly to an increase of radial growth in the region between the growing-point and the wound. The lower part of this region abutting on the wound may be occupied by the reuniting flanks of P_1 , or it may remain unoccupied and is then marked with radial cell rows. The cathodic flank of I_1 was not seen to occupy the lower part of this region, even when it was not occupied by P_1 , but this flank of I_1 did appear to occupy the upper part nearer to the apex. It could not be seen in these observations made in the solid whether the centre of I_1 had been displaced towards the wound, but such a displacement could be understood on the basis of a space-filling theory, since the increased radial growth between the wound and the growing-point provided additional space in that part of the apical cone.

A real displacement of I_1 towards the original centre of P_1 , caused in this way, will of course diminish the angle P_1-I_1 , calculated from P_2-I_1 , and this change will be added to

the change of this angle in the same sense which, as explained above, is due simply to the shift of the apical centre from which it is measured.

Similar observations were made after removal of the centre of P_2 in five apices. In all five the apex was seen to broaden transversely in the median plane bisecting the wound, and radial rows of cells were seen abutting on the wound suggesting that the shift of the growing-point had taken place in the same manner as when the centre of P_1 was removed. In two of these apices the region of radial extension was occupied by the cathodic flank of P_1 within 7 days of the operation. In two others, in which P_1 did not encircle the apex until 8 and 15 days respectively, this region remained unoccupied. This supports the above suggestion that the region of radial extension remains unoccupied unless it is occupied within 7 days of the operation. These observations also account for the thickening of the cathodic flank of P_1 after removal of the centre of P_2 which will be described in §4.

It may be left an open question whether in *Rhoeo* the shift of the growing-point is due only to the increased radial growth of the part of the apical cone above the wound, or whether it is due partly to another process, in which the original growing-point is replaced by a new one formed farther from the wound. The latter was considered to be the chief factor displacing the growing-point in *Lupinus albus* (Snow & Snow 1931).

The interpretation of the results so far discussed in terms of shift of the growing-point and space-filling theory are further supported by the results of a different operation in which the greater part of the anodic half of P_1 was removed by a cut, instead of its central part (figures 12, 13, p. 62). The extent of the part removed is shown cross-hatched on a section of a normal apex in figure 11 (p. 62). For in six out of eleven apices so treated, the first six reported in table 2, the angle P_1-I_1 decreased very considerably, its mean decrease being 16.3° and a considerable shift of the growing-point away from the wound was indicated by an increase of the angle P_2-P_1 , measured above the insertion of P_1 , in three of these six (table 2, column 3), while in two of them it could not be measured. But in the next three operations of the table, the angle P_1-I_1 was normal, or in one even slightly increased, and the angle P_2-P_1 was also about normal, indicating no displacement of the growing-point. Thus these first nine operations provide further evidence indicating that a decrease in the angle P_1-I_1 is associated with a shift of the growing-point in the direction which would cause it to decrease. The results would be difficult to explain on the repulsion theory, since the repulsions were supposed to come from the centres of the young leaves, and no such centre was removed. The last two apices of table 2 are not comparable, since in them I_1 arose on the other side of P_1 .

To summarize the conclusions reached so far, if the two interpretations of the results of the operations so far reported are compared, the repulsion theory proposed previously accounts for the displacement of I_1 towards P_1 after removal of the central part of P_1 , but fails to account for the fact that I_1 was displaced the other way very little, if at all, when the central part of P_2 was removed, unless the part removed was very large. But a space-filling theory can account for both results, since it has now been shown that the growing-point of the apex shifts away from the wound when the central part of P_1 is removed, but that it does not do so, or only slightly, when the central part of P_2 is removed, unless the part removed is very large. This shift of the growing-point will cause an apparent displacement of I_1 towards the removed leaf centre. It may also have caused a real displacement

TABLE 2. ELEVEN APICES IN WHICH PART OF THE ANODIC HALF OF P_1 WAS REMOVED

All measurements in degrees.

numbers of apices	size of P_1 when operated	divergence angles					anodic eccentricity of bud of P_1 (normal 5°)	arcs of anodic halves of leaves			strand number ratio a/k of I_1
		P_2-P_1	P_1-I_1	I_1-I_2	I_2-I_3	I_3-I_4		I_1	I_2	I_3	
apices with I_1 on the anodic side of P_1											
291	small medium	173	122	217 143}	154	141	15	201	165	166	1.25
284	small medium	—	130	162	147	146	12	162	170	169	0.91
289	small medium	160	135	185 175}	135	156	21	195	176	179	1.44
295	small medium	165	144	174	144	159	14	178	160	180	1.0
282	small medium	—	144	193 167}	140	161	16	188	158	174	1.0
292	medium large	153	145	169	143	—	9	173	164	173	1.0
293	large	150	155	164	143	156	15	162	165	167	0.93
286	medium large	147	154	167	144	150	—	165	167	173	0.87
287	small medium	151	154	169	142	—	10	180	170	173	0.92
apices with I_1 on the cathodic side of P_1											
290	small medium	179	201 159}	133	165	125	21	92	173	—	—
294	medium large	170	230 130}	144	142	158	21	158	169	175	—

Notes. (1) Where a divergence angle exceeds 180° measured in the original direction of the spiral and the spiral continues in the reversed direction, the supplementary smaller angle is bracketed with the larger angle and subsequent angles are measured in the new direction of the spiral.

(2) The half of a leaf called anodic is always the half which is farther from the centre of the previous leaf.

of I_1 in that direction when the centre of P_1 was removed, since short-time observations after these operations made it appear probable that the space available upon the apex was increased above the wounds. It has also been shown that the decrease of the angle P_1-I_1 after some of the removals of the anodic flank of P_1 can be explained much more easily in terms of the shift of the growing-point and of space-filling theory than on the repulsion theory.

The positions of I_2 and I_3 after these operations, and certain changes in the asymmetries of various leaves, will be discussed below, when the new space-filling theory of the normal phyllotaxis of *Rhoeo* has been proposed. Also the results of removing the anodic flank of P_1 will be further described and discussed in §5.

3. A NEW INTERPRETATION OF THE NORMAL PHYLLOTAXIS OF *RHOEO*

Since the experimental results discussed above can be explained on a space-filling theory, but not on the theory of physiological repulsions, the question arises whether after all the normal spirodistichous phyllotaxis of *Rhoeo* can be explained on a space-filling theory. It may be significant that spirodistichy is commonly, or perhaps always, associated with leaves which encircle the apex at their bases (amplexicaul leaves), and so also is spiromonostichy, as in *Costus*. On the other hand, straight distichy is nearly always associated with leaf bases that cover less than 360° , but more than 180° , before the end of

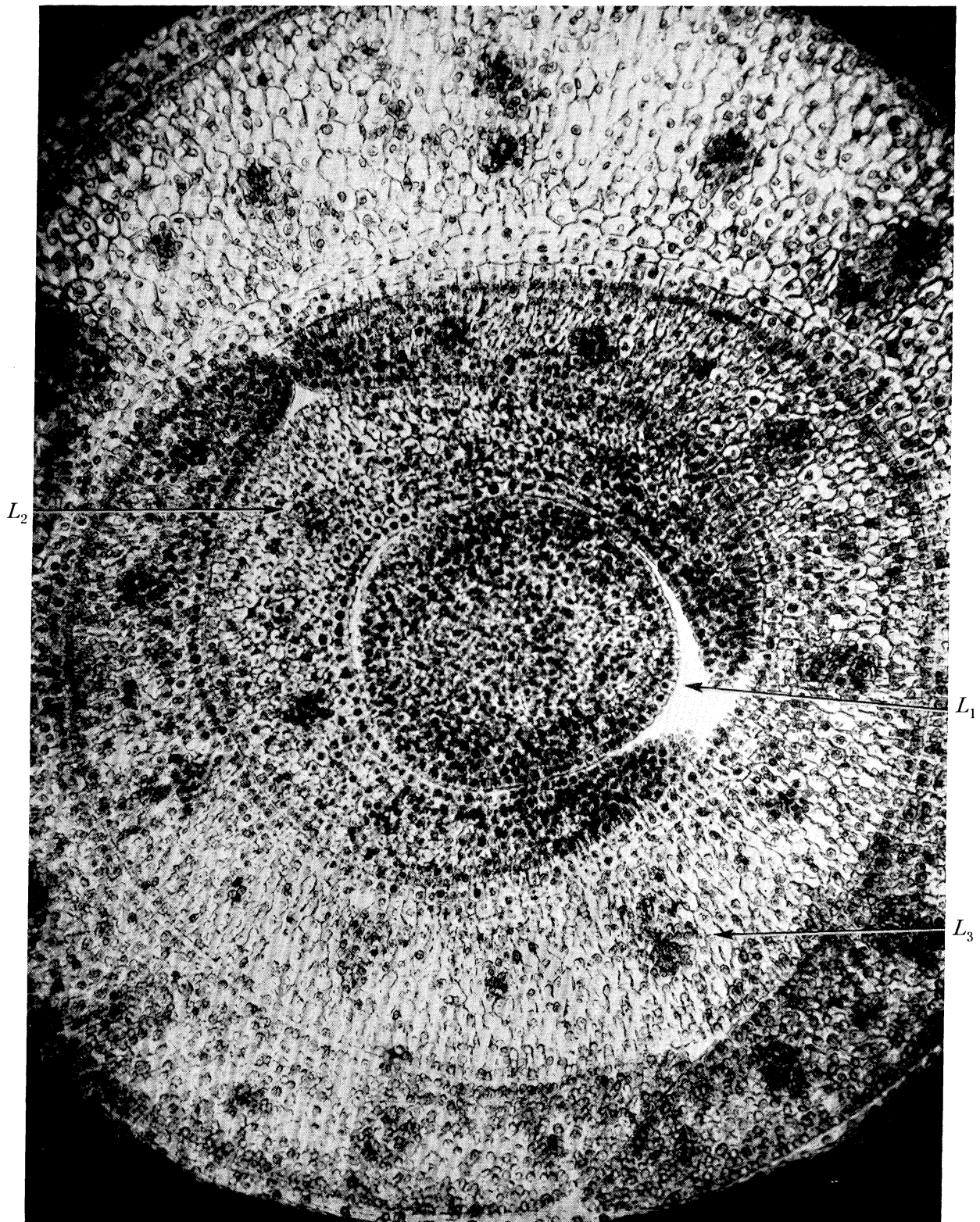


FIGURE 8. Photograph of a transection of a normal apex of *Rhoeo discolor* just above the insertion of the second youngest leaf. The genetic spiral wound clockwise. The arrows L_1 , L_2 and L_3 point to the centres of leaves one, two and three respectively. (Magn. $\times 152$.)

(Facing p. 57)

their first plastochrons. This suggests that spirodistichy somehow depends on the flanks of the leaves, which encircle the apex, and in *Rhoeo* these flanks have been found to have peculiar powers of development. Thus after a series of operations in which the apex was split in a plane at right angles to the median plane through P_1 , it was found that if the tips of the flanks of P_1 extending gradually round the apex had reached the farther half of the apex before the operation, they continued to extend round the farther half independently, though they were now separated from the central part of P_1 , as was more fully described in the previous paper (1951, pp. 156, 157). Also in an early series of operations several attempts were made to block the extension of the flanks of P_1 by means of radial cuts in the leaf-forming zone, in order to find out how the subsequent phyllotaxis would be affected. But the flanks always changed their directions of growth and extended over the apical end of the cut, between the cut and the summit of the apex, showing that they can grow closer to the summit when they meet an obstacle. So the gradual extension of the leaf flanks in *Rhoeo* follows a different rule from that which was found to hold good for the determination of the primary area of a leaf in *Lupinus albus* (Snow & Snow 1931, 1933). For the primary area in *Lupinus* was found to be determined as a whole in the first sufficient space, and the same may be true for some central primary leaf area in *Rhoeo*, as will be discussed below, though not for the leaf flanks.

Since the leaf flanks in *Rhoeo* can extend in this peculiar manner, it was very valuable to the writer to receive a letter from Professor G. van Iterson in April 1951, in which he also considered it significant that in *Rhoeo* each leaf encircles the apex, and further suggested that the cause of the deviation from straight distichy is that the position of any new leaf, n , is somehow affected by the bud in the axil of the leaf that is two plastochrons older, $n-2$, which prevents leaf n from arising on or near the same radius and displaces it to one side. It seems to the writer necessary to take into account not only the axillary bud, but the central part of leaf $n-2$ itself, which, being the thickest part of the leaf, approaches at its insertion more closely to the stem apex than do the lateral parts of the leaf. But with this addition the new suggestion combines very well with the above observations on the extension of the leaf flanks. For since a flank of a leaf grows towards the summit of the apex when it meets a radial cut, and so passes over it, the cathodic flank of leaf $n-1$ may be expected to do the same when it meets the obstacle of the uprising central part of leaf $n-2$ (see figure 1), together with its axillary bud, of which the rudiment has been seen to be present before leaf n arises. Consequently the upper contour of the cathodic flank of leaf $n-1$ will be higher—that is, closer to the growing-point of the apex—where that flank passes over the central part of leaf $n-2$ than elsewhere. So if the primary area of each new leaf is determined in the first sufficient space, leaf n will arise with its centre not opposite the centre of leaf $n-1$ (see figure 1), since there it would be too close to the hump in the flank of leaf $n-1$ over the central part of leaf $n-2$, but some way to one side. Further, it is clear from figure 1 that leaf n will deviate in the same direction as did leaf $n-1$ previously, and so the spiral will continue.

Direct evidence of the rising up of a leaf flank over the central part of the previous leaf is provided by the photograph of a transection of a normal *Rhoeo* apex shown in figure 8, plate 1. It can be seen that where the flank of the leaf L_2 passes over the centre of the next older leaf, its contour becomes almost straight, instead of continuing the curve.

Thus in this region the leaf flank approaches more closely to the growing-point, and so is morphologically higher than elsewhere. The normal asymmetry of the leaves, of which the anodic half covers a smaller arc but is thicker radially, will be discussed in §9.

4. THE CHANGES IN SHAPE OF LEAVES DIRECTLY ABOVE WOUNDS AND THEIR EFFECTS ON THE POSITIONS OF SUBSEQUENT LEAVES

It may now be considered how the positions of the subsequent leaves I_2 and I_3 in these experiments can be interpreted. When the central part of P_1 was removed, the angle I_1-I_2 increased considerably, and in three apices exceeded 180° . Its increase was interpreted previously as being due to a repulsion of I_2 by the centres of I_1 and P_2 , which became more effective when the opposing centre of P_1 was removed (Snow, M. 1951, table 2 and figure 6). But now that the repulsion theory has been found to be unsatisfactory, since P_2 seems not to repel, a new interpretation will be suggested.

It is suggested that the shift of the growing-point away from the wound displaced I_2 towards the original centre of P_1 and increased the angle I_1-I_2 in the same two ways in which it displaced I_1 towards the centre of P_1 and diminished the angle P_1-I_1 . This is to be expected if the growth changes displacing the growing-point continue after I_1 has been determined; and it seems probable that they do so continue. For the flank of I_2 over the wound, as well as the flank of I_1 over the wound, was often quite abnormally thick (see 1951, figures 3c, 4a, 7c); and this thickening can reasonably be considered to be due to an increase of radial growth above the wound continuing long enough to affect I_2 . It will be further discussed below.

But the displacement of I_2 towards P_1 may also have been due partly to a change in the peripheral extensions of the flanks of I_1 , of which leaf the anodic flank covered an arc larger than the normal arc of 166.5° (see 1951, table 2), while the cathodic flank covered a correspondingly smaller arc than normal (1951, table 3, column 2). The mean anodic arc of I_1 after the previous removals of P_1 centres together with no. 265 of the present paper was 180.9° . This change in shape of I_1 was indeed closely correlated with the displacement of I_2 indicated by the increase of the angle I_1-I_2 , as was pointed out in the previous paper (1951, p. 154 and figure 10). It brought the meeting-point of the edges of I_1 closer to the original centre of P_1 ; and since this meeting-point is a low point towards which the contour formed by I_1 round the apex slopes downwards, the central part of I_2 may be expected on space-filling theory to be displaced in the same direction.

The change in shape of I_1 can itself in turn be explained as being due to the shift of the growing-point: but first it must be noted that since the flanks of a leaf extend round the apex until they meet, an increase or decrease in extension of either flank leads to the opposite change in the other flank. The cathodic flank of I_1 , which is decreased in extension, lies above the removed centre of P_1 and is therefore the flank which is most likely to be affected primarily by the operation. This flank was also regularly seen to be increased in radial thickness (see for example figure 9 and 1951, figures 3, 4, 5), and a radial thickening of a part of a leaf above a wound, which has often been found in other species, may well be explained as due to the increase of available space above the wound associated with the shift of the growing-point. After other operations also in *Rhoeo* it has often been

found that the radially thicker half of I_1 over the wound is peripherally the shorter, and similarly in normal apices the anodic half of each leaf is both radially thicker and peripherally shorter. It may therefore be suggested that in leaves of *Rhoeo* radial thickening diminishes tangential extension, perhaps by using up in a different way something necessary for growth.

Previously the writer suggested (1951, p. 155) that the correlation between the decrease in peripheral extension of the cathodic flank of I_1 and the displacement of I_2 towards the removed centre of P_1 was due to the removal of some physiological influence from that leaf centre which normally promoted the extension of leaf flanks but repelled

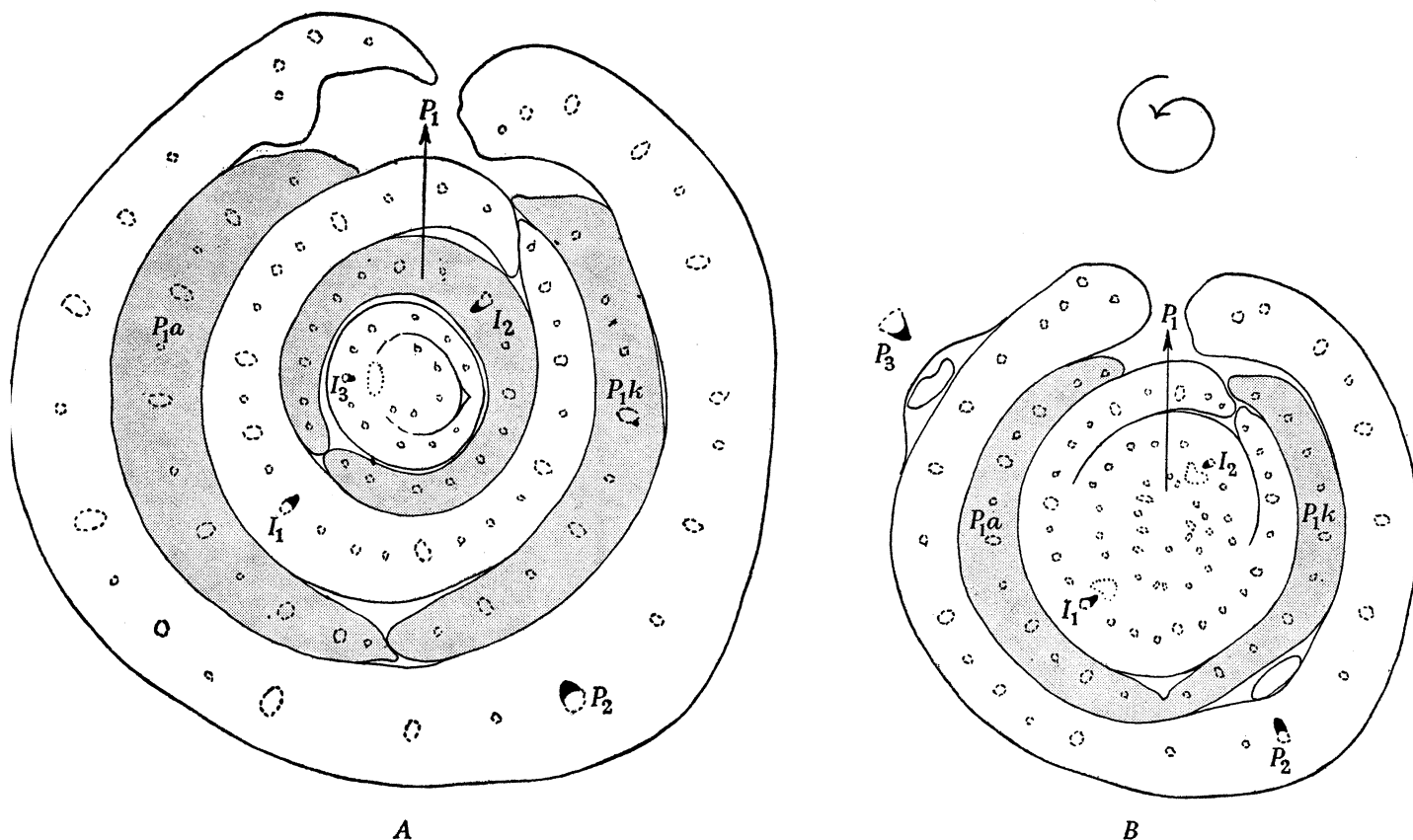


FIGURE 9. *A* and *B* are transections of no. 265. The centre of P_1 was removed.
(Magn. *A*, $\times 34$; *B*, $\times 22$.)

new leaf centres. The correlation still seems well established, and indeed is further supported by new experiments to be reported below; but it can be interpreted more easily as above, as being due to the shift of the growing-point, associated with increased radial growth above the wound working in the two ways explained. For this changes both the position of I_2 and the shape, as well as the position of I_1 .

Similarly, when the central part of P_2 was removed and I_1 appeared to be displaced towards the wound, this displacement may have been not only an apparent one due to the shift of the growing-point, as already discussed, but also partly a real displacement due to a change in the shape of P_1 . For in the apices of series 3 of table 1, and in the last four apices of series 1, which were those in which I_1 appeared to be considerably displaced towards the wound, the cathodic half of P_1 over the wound was thickened radially and

shortened peripherally (see figure 4A, no. 224), just as was the cathodic half of I_1 when the central part of P_1 was removed. The peripheral shortenings of these cathodic halves of P_1 are indicated by the corresponding increase of the arcs of the anodic halves recorded in table 1, column 8. In most of the other apices these changes were smaller.

The displacements of I_1 towards the wound after removal of P_2 , indicated by the increases of P_1-I_1 were indeed closely correlated with the increases in the extensions of the anodic halves of P_1 , indicating decreases of the cathodic halves as is shown graphically in figure 10. Similarly, after the previous removals of the central part of P_1 the displacements of I_2 were correlated with the corresponding changes in the flanks of I_1 (1951, figure 10).

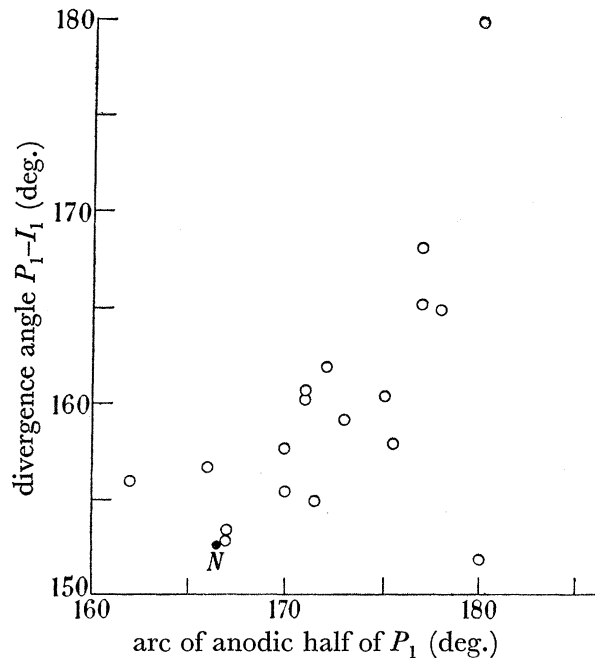


FIGURE 10. Graph showing the relation between angle P_1-I_1 (ordinates) and arc covered by anodic half of P_1 (abscissae) in apices in which the centre of P_2 was removed. The dot N shows the mean normal values of a divergence angle and of the anodic half of a leaf.

The radial thickening of the cathodic flank of P_1 in the apices of series 3 of table 1, and in the last four apices of series 1, was very conspicuous and seems to have been due partly to the fact that in none of these apices except two, nos. 133 and 132, did the remaining portions of the P_2 's reunite by regenerating above the wound. Consequently more of the space above the wound provided by the increased radial growth of the stem apex in this region was available for the flank of P_1 .

The peripheral shortening of the halves of the leaves above the wounds must indeed in many of the apices have been in part an apparent change only, due to the shift of the growing-point, from which their arcs were measured, away from the wound. But counts of the numbers of vascular strands in the halves of these leaves and comparisons with those of normal leaves indicate that some part of the peripheral shortening above the wounds was real.

The number of strands increases slowly with age, but in eighteen leaves which belonged to normal apices and were about as old as were the I_1 and P_1 leaves of the experiments

when examined, it was found that in the peripherally shorter anodic halves, though these are radially the thicker, the mean number of strands was less, being 9.44, whereas in the cathodic halves the mean was 11.61. The ratio a/k of the means was 0.81, with $\sigma=0.09$ and $\sigma_m=0.02$. On the other hand, in nine apices with centre of P_1 removed the mean strand ratio a/k in the I_1 's was 1.03, with $\sigma=0.25$, and $\sigma_m=0.08$, and only in one of them, no. 6 of 1951, was the ratio less than unity. Clearly, therefore, in these I_1 's the anodic halves were abnormally long and the cathodic halves over the wounds abnormally short.

Similarly, in the six apices of series 3 of table 1 in which the central part of P_2 was removed with a severe operation, the mean strand ratio in the P_1 's was 1.035, with $\sigma=0.10$ and $\sigma_m=0.041$, and in none of these was the ratio less than unity. So in these apices also the cathodic half-leaf above the wound was clearly peripherally shortened. But in six apices of series 2 of table 1, in which the change of shape of P_1 was much less, the mean strand ratio a/k , was 0.90, with $\sigma=0.083$ and $\sigma_m=0.034$, which is much closer to normal. (In one more apex of series 2, no. 144, the strands could not be counted accurately.)

There remains to be considered the unusual position of I_3 in some of the apices in which the centre of P_1 was removed. For in three of these apices described in the previous paper (1951, p. 149, figs. 4D, 5A, C and table 2), and in one described here (no. 265, figure 9 and p. 51) the angle I_1-I_2 measured in the original direction of the spiral exceeded 180° , but I_3 arose in the smaller angle between I_1 and I_2 , and so was on the usual side of the apex. This position of I_3 , which was interpreted previously as due to a repulsion from the centre of P_2 , agrees with the rule that the side of the apex above the wound is favourable to formation of leaf centres, though unfavourable to extension of leaf flanks. Moreover, the flank of I_2 above the wound was the thicker radially and the shorter peripherally, which agrees with the rule concerning the flanks of leaves above wounds noted already. Both these effects could be attributed to a shift of the growing-point, associated with an increased radial growth of the apex above the wound, continuing up to and even after the determination of I_2 . But it is not known whether the growing-point continues to shift even after I_2 is determined, though the change in shape of I_2 indicates that it does continue to shift up to this time.

5. THE APICES IN WHICH PART OF THE ANODIC FLANK OF P_1 WAS REMOVED

It has been mentioned in §2 that in the first six apices of those recorded in table 2, p. 56, in which part of the anodic flank of P_1 was removed, the angle P_1-I_1 was diminished; and that the angle P_2-P_1 , in three out of four of these apices in which it could be measured, was greatly increased, indicating that the growing-point had shifted away from the wound. In several of these apices the apical cone was seen a few days after the operation to be broadened in the plane passing through the wound. In the next three apices of the table neither of these changes of angle occurred. The subsequent changes in all the apices operated upon in this way must now be considered.

The angle I_1-I_2 was much increased in all the first nine apices of table 2 (see column 5 and figures 12, 13), indicating that I_2 was displaced towards the wound, as I_1 also had been in some of these apices. In three of them the angles I_1-I_2 even exceeded 180° , and in these nos. 291, 289 and 282) the spiral continued reversed (figure 12). The displacement of I_2 may have been caused in the first six apices, partly at least, by a shift of the growing-point

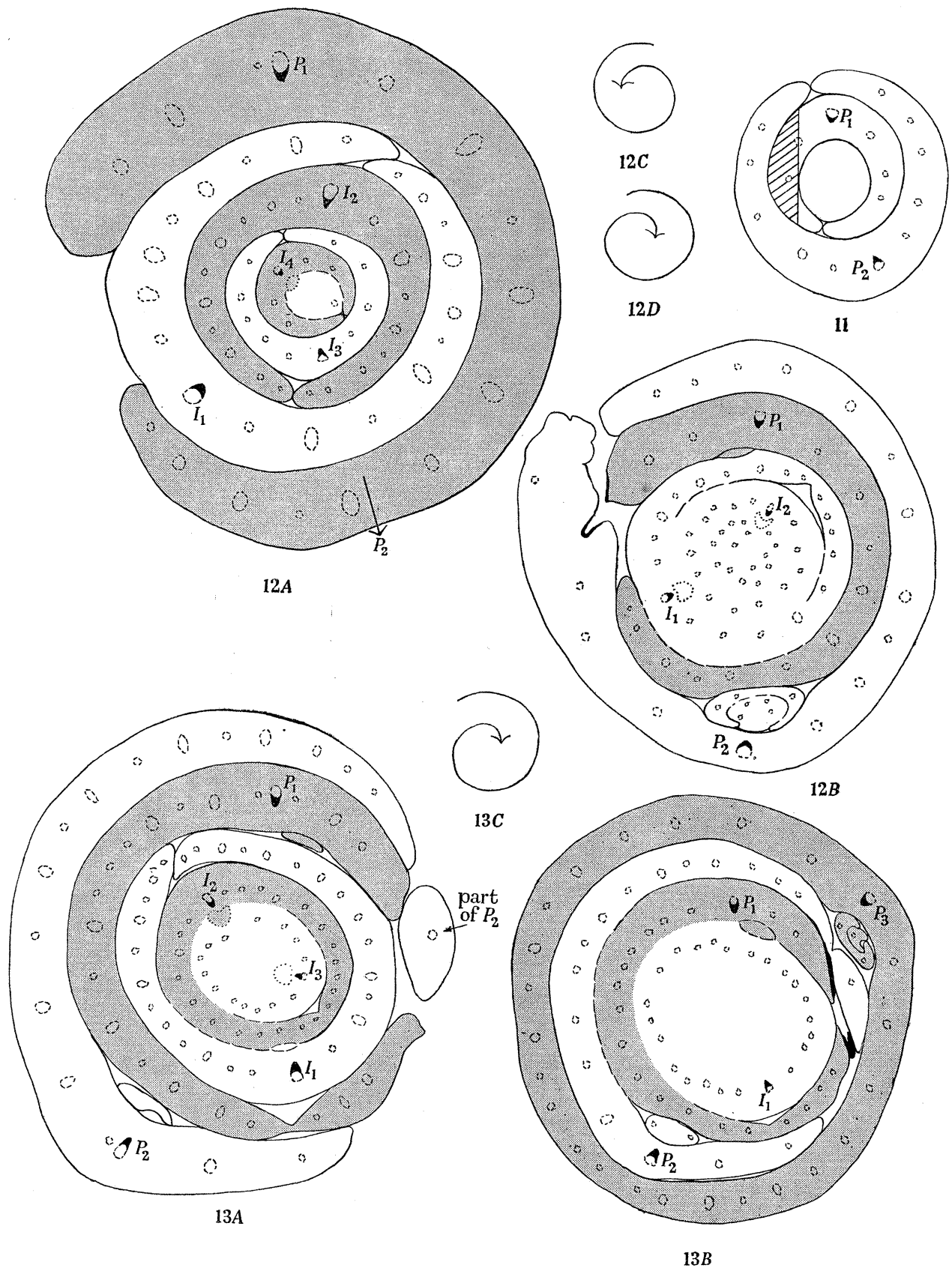


FIGURE 11. Diagram to show the part of the anodic flank of P_1 that was removed, as seen in transverse section. The shaded part was removed.

FIGURE 12. *A* and *B* are transections of apex no. 291 from above downwards. Part of the anodic flank of P_1 was removed. I_1 arose on the usual (anodic) side of P_1 . In *B* the cathodic flank of P_2 has developed abnormally, being injured. *C* and *D* show the original and final directions of the genetic spiral respectively. In this and subsequent figures an arrow indicates the position of the centre of an outer leaf not included in the drawing. (Magn. *A*, $\times 40$; *B*, $\times 22$.)

FIGURE 13. *A* and *B* are transections of apex no. 293 from above downwards. Part of the anodic flank of P_1 had been removed. I_1 arose on the usual (anodic) side of P_1 . The extreme edge of the anodic flank of P_1 has developed independently beyond the part removed. (Magn. *A*, $\times 22$; *B*, $\times 16$.)

continuing after I_1 was determined. Another factor displacing I_2 was probably the change in shape of I_1 , of which the flank that was anodic in the original direction of the spiral often extended peripherally in these apices much more than is normal (column 9). For as a result of this change the junction of the flanks of I_1 was shifted round towards the wound (see figure 12, no. 291), and since this junction is a low point in the contour round the apex, the centre of I_2 may have shifted in the same direction in consequence. This was also suggested in §4 to be one factor causing the displacement of I_2 towards the wound when the centre of P_1 was removed. The change in shape of I_1 after these operations, as after the previous ones, seems to have been due to a radial thickening of its cathodic flank, often clearly visible, in the region above the wound (see figure 12), which led according to the rule already suggested to a peripheral decrease of that flank and so to an increase of the other flank.

Counts of the strands in the halves of I_1 in these nine apices showed that, just as in the apices discussed in §4, the peripheral shortening of the cathodic half of I_1 above the wound was real, at least in part, and not merely an appearance due to the shift of the growing-point. For the mean ratio, a/k , of the numbers of strands in the anodic and cathodic halves of I_1 was 1.04, with $\sigma=0.018$ and $\sigma_m=0.054$, as against the normal 0.81, with $\sigma=0.089$ and $\sigma_m=0.021$.

But two of the nine apices, nos. 293 (figure 13) and 286, were exceptional in that neither of the two factors mentioned can account for the increases of the angles I_1-I_2 in them. For the growing-point was found not to have shifted, and the arc covered by the anodic half of I_1 was within the normal range (see table 2). The increases of the angle I_1-I_2 were not indeed large in these two apices, being only 11° and 14° above the normal; but still they were definite, so that there must have been still a third factor at work in causing the increase of this angle. This third factor seems to have been an increased eccentricity of the axillary bud of P_1 . For whereas in normal *Rhoeo* apices the axillary buds are displaced only slightly from the centre of the subtending leaf in the anodic direction, their mean eccentricity being 5° , in eight of the present nine apices the eccentricity of the bud of P_1 ranged from 9° to 21° , the mean being 14° (table 2, column 8). As to the two apices in which no other cause was found for the increase of the angle I_1-I_2 , in no. 293 the bud of P_1 was 15° eccentric, and in no. 286 it could not be found and may have been lacking.

It may be recalled that reasons were given in §3 for thinking that in normal *Rhoeo* apices the central part of any leaf n , together with its axillary bud, by approaching closer to the summit of the apex, causes the cathodic flank of the next leaf, $n+1$, to grow closer to the summit of the apex in extending over these obstacles; and that this in turn causes the centre of leaf $n+2$ to be displaced to one side (the cathodic side) of the same angular position (see figure 1). So when, as in the present apices the bud of P_1 is displaced in the anodic direction or is lacking, as probably in no. 286, it may be expected that it will not displace the centre of I_2 so far as usual in the cathodic direction, and so the angle I_1-I_2 will be increased. The eccentricities of axillary buds will be discussed in §10.

In the last two apices of table 2, nos. 290 and 294 (figures 14, 15), I_1 was displaced to the opposite side of the apex from the normal, where it arose in the smaller angle between the centres of P_2 and P_1 . This reversed the spiral, which continued reversed in both apices.

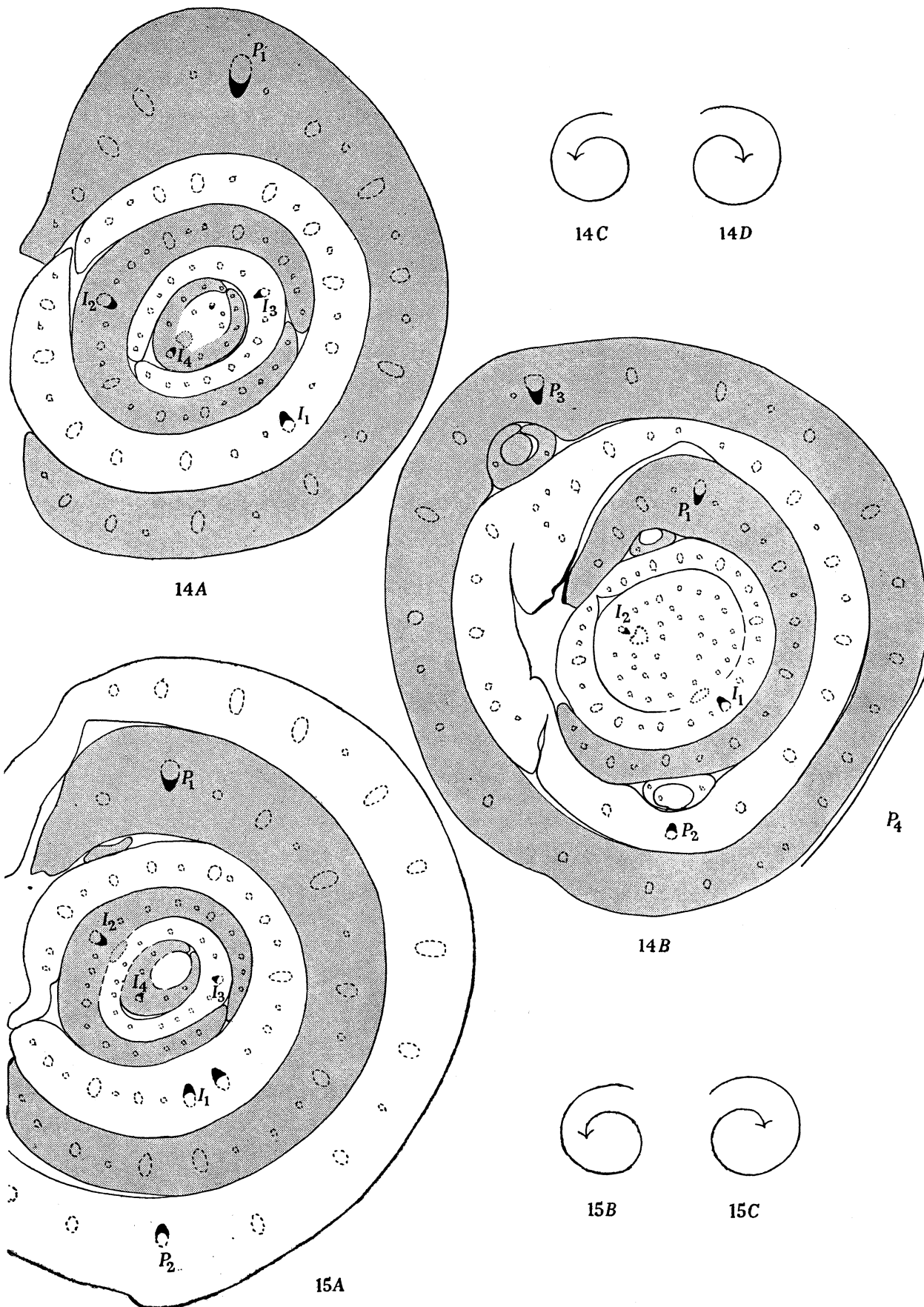


FIGURE 14. *A* and *B* are transections of apex no. 294 from above downwards. Part of the anodic flank of P_1 has been removed. I_1 arose on the other side of the apex from the normal. In *B* the cathodic flank of P_2 has developed abnormally, being injured. The two small spirals in this and in subsequent apices with reversals, show the original and final directions of the genetic spiral. (Magn. *A*, $\times 31$; *B*, $\times 18$.)

FIGURE 15. *A* is a transection of apex no. 290. Part of the anodic flank of P_1 had been removed. I_1 arose on the other side of P_1 from the normal and had two strands instead of a median strand. (Magn. *A*, $\times 28$.)

The probable explanation is that the cut had encroached upon the presumptive area of I_1 , as it was seen at the time of operation to have done. In these two apices the growing-point had again been displaced away from the wound, as is shown by the increased angle P_2-P_1 (table 2, column 3). The angular distances of the centre of I_1 from that of P_1 were about the same as in the other apices of table 2, but cannot well be compared with them, since I_1 was situated differently in relation to P_1 and to the wound.

However, the angle I_1-I_2 in nos. 290 and 294 is of interest as a test of the explanation suggested for its increase in the other nine apices. The shift of the growing-point away from the wound, with the associated broadening of the apical cone, would not directly affect the angle I_1-I_2 much in nos. 290 and 294, since the centre of I_2 came somewhere over the wound, instead of coming to one side of it. But the greatly increased eccentricities of the buds of P_1 , which were both 21° eccentric, would in these two apices tend to decrease the angle I_1-I_2 instead of increasing it, by displacing I_2 away from the centre of P_1 instead of towards it. For I_2 was here on the same side of P_1 as the bud of P_1 (see figures 14, 15). Also the change in shape of I_1 , of which the flank nearer to the wound was again shortened peripherally and thickened radially, would in these two apices, by shifting the junction of the flanks of I_1 , tend to displace the centre of I_2 in the same direction, that is, away from P_1 . So both these factors would tend to decrease the angle I_1-I_2 ; and the suggestion that in the other nine apices one or both of these two factors tended to increase the angle I_1-I_2 is strongly supported when it is found that in nos. 290 and 294, with I_1 on the other side of P_1 , this angle was much decreased (to 133° and 144°) instead of being increased, as in all the first nine apices.

It may be mentioned that in no. 290 (figure 15) I_1 had, instead of a central strand, two strands of similar appearance only 16° apart. Angles were measured from a line midway between them. This leaf was also very asymmetric.

It may also be mentioned that the part of the anodic flank of P_1 beyond the cut did not develop, except in nos. 292 and 293 (figure 13), and that consequently in the other apices of table 2 the cathodic half of P_1 was able to extend far beyond its usual length and covered arcs ranging from 233° to 287° , instead of the normal 193.5° . Also one flank of P_2 was often injured by the cut and could be seen to have grown abnormally, as in no. 291, figure 12 (p. 62).

6. THE APICES IN WHICH I_1 WAS DIVIDED BY A RADIAL CUT

Further evidence concerning the location of leaf centres in *Rhoeo* is provided by ten apices in which the presumptive area of I_1 was divided with a vertical radial cut passing through its centre, or sometimes with a needle prick in the same position. The main results are given in table 3. The operation was a prick in nos. 44, 52 and 49, and a cut in the other apices. An advantage of these operations is that they apparently do not displace the growing-point away from the wound, as was shown by the angles P_3-P_2 and P_2-P_1 , which in three apices in which they could be measured, nos. 44, 83, 125, were respectively 150° , 154° , 156° and 157° , 154° , 149° . Unfortunately, in the other apices of table 3 these angles could not well be measured, since P_2 had been too much injured by the cut.

The results were briefly as follows: In the first two apices of table 3 the centre of I_1 was displaced considerably (35° and 21°) in the cathodic direction by the cut (figure 16,

TABLE 3. TEN APICES IN WHICH THE PRESUMPTIVE AREA OF I_1 WAS DIVIDED RADially

numbers of apices	size of P_1 at operation	divergence angles					angle I_1 -wound	arcs of anodic halves of leaves			
		P_1-I_1	I_1-I_2	I_2-I_3	I_3-I_4	I_1		I_2	I_3	I_4	
apices with I_1 on the cathodic side of the wound											
44	very large	118	170	145	158	28	178	171	172	165	
52	very large	132	164	141	153	29	180	171	161	166	
apices with I_1 on the anodic side of the wound											
83	small medium	249 111	173	—	—	109	180	168	—	—	
85	medium large	235 125	158	140	147	85	173	—	—	—	
49	large	263 97	156	151	154	96	166	177	171	173	
84	large	225 135	180	145	159	83	201	174	176	168	
125	large	261 99	151	146	159	110	—	168	169	163	
126	small medium	257 103	178	130	155	132	171	164	167	172	
apices with I_1 double having a cathodic centre (I_1k) and an anodic centre (I_1a)											
		divergence angles					angle I_1k -wound	arcs of anodic halves of leaves			
		P_1-I_1a	I_1a-I_1k	I_1k-I_2	I_2-I_3	I_3-I_4		I_2	I_3	I_4	
120	small medium	253	170	94	165	144	56	165	179	—	
121	very small	261 99	137	148	168	143	46	165	180	179	

See notes (1) and (2) to table 2, p. 56.

no. 44). In the next six apices it was displaced still further, but in the anodic direction, to positions that were all well beyond the centre of P_2 (figure 17, no. 49). This reversed the spiral which continued reversed in all six. In the last two apices I_1 was a double leaf with two morphological centres, one on each side of the cut. The spiral reversed in one of these two.

The chief point of interest in these results is that the centre of I_1 when displaced in the anodic direction was always displaced well beyond the centre of P_2 , so that it seemed to avoid a position over that centre. For its mean displacement from its normal position in the eight apices which formed an I_1 centre on the anodic side of the wound, including the two with double I_1 's, was 96.5° , the least displacement being 71.9° in no. 84; and these displacements brought the anodic I_1 centre to a mean angular distance of 41.7° beyond the estimated original position of the centre of P_2 , the least distance beyond it being 17.1° in no. 84. On the other hand, in the four apices which formed an I_1 centre on the cathodic side of the wound remote from the centre of P_2 , including again the two with double I_1 's, the mean cathodic displacement of the I_1 centre from its normal position was only 27.7° . This is strong evidence that in *Rhoeo* the centre of any new leaf n does indeed avoid a position over or nearly over the centre of leaf $n-2$, although separated from it by a flank of leaf $n-1$. Hence it may be concluded that it is indeed this factor that makes the normal phyllotaxis spirodistichous.

Yet these results, like those already discussed, make it unlikely that the influence from the centre of leaf $n-2$ is a physiological repulsion, since this leaf, which here was P_2 , was cut down very nearly to its base in these operations, about as far down as in the less severe

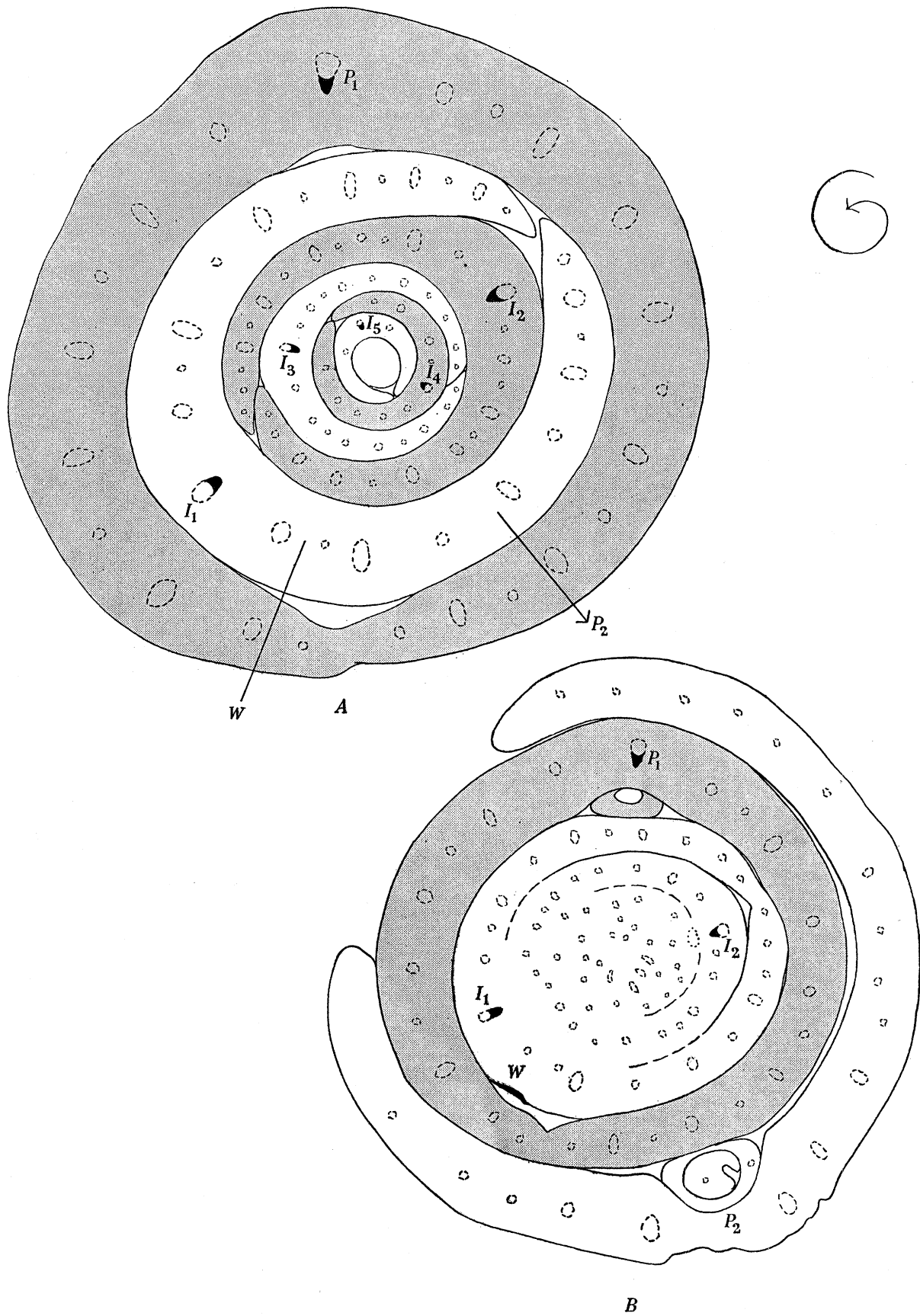


FIGURE 16. *A* and *B* are transections of apex no. 44. The presumptive area of I_1 was divided radially with a prick. I_1 arose on the cathodic side of the wound. In this and subsequent figures the wound scar is marked *W* and the angular position of the wound is shown in sections above the scar by the line *W*. (Magn. *A*, $\times 30$; *B*, $\times 20$.)

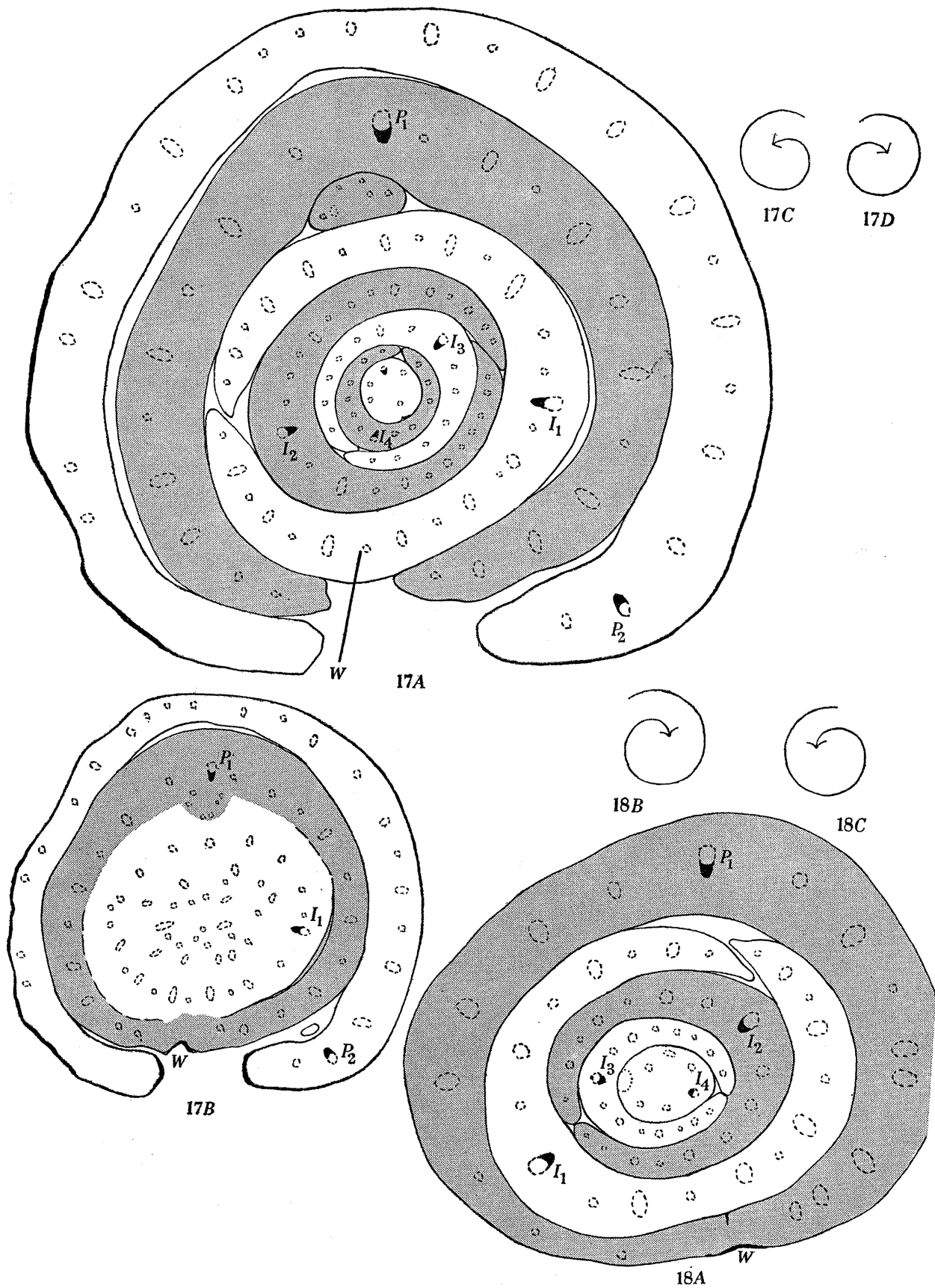


FIGURE 17. *A* and *B* are transections of apex no. 49. The presumptive area of I_1 was divided radially with a cut. I_1 arose on the anodic side of the wound. (Magn. *A*, $\times 27$; *B*, $\times 14$.)

FIGURE 18. *A* is a transection of apex no. 84. The presumptive area of I_1 was divided radially with a cut. I_1 arose on the anodic side of the wound. (Magn. *A*, $\times 41$.)

removals of the P_2 centres (table 1, series 2). This was done in order to expose the apex. But the axillary bud of P_2 always developed, and the leaf base remained and developed in all the apices except nos. 126 and 121; and one or both of these members may well have contributed to displacing I_1 by causing the flank of P_1 to rise up over the central part of P_2 in the manner suggested in §3.

Another point to be noted is that an I_1 centre was never formed close to a cut, although the cut was made as nearly as possible through the presumptive position of that centre (table 3, column 7). This was also found to be so after the same operation on *Lupinus albus* (Snow & Snow 1933, 1952), except sometimes when the operation was made at late plastochron and I_1 was probably partially determined. It was concluded that the centre of a completely new leaf must be determined at a distance from a cut sufficient to allow room for the half of its primary area on that side. The same conclusion holds good for *Rhoeo*, although it seems that in the *Rhoeo* leaves, of which the flanks extend so vigorously, the primary area is much smaller in relation to the whole leaf base. Also in the first two apices of table 3, in which the distance of the I_1 centre from the cut was least (28° and 29°), the operation was made at very late plastochron, so that I_1 may have been partially determined, and closer to the cut for that reason. The distance from the cut of the other two cathodic I_1 centres, which were in the apices with double I_1 's, were 56° and 46° . In any case all these measurements provide only minimum values for the half of the primary leaf arc, since some part of the primary area may have lain directly above the wound. But they are enough to show that in *Rhoeo*, as in *Lupinus albus* and other apices, some primary area is determined as a whole and not the leaf centre first, as has been suggested. The anodic I_1 centres were much farther still from the cut, but since they were displaced beyond the central parts of the P_2 's, their distances from the cut do not signify.

The angular distance of the cut from the centre of P_1 can be calculated from columns 3 and 7 of table 3. It was intended to place the cut at just the normal mean angle of 152° from the centre of P_1 , but in this species the exact positions of the leaf centres cannot be seen in the solid and when the apices were sectioned the distance of the wound from P_1 was found to vary considerably.

It may be noted that in these apices when I_1 was single its axillary bud always deviated from the leaf centre in the direction away from P_1 , which was also the direction of the subsequent spiral. This was so even when I_1 arose on the other side of P_1 from the normal, even when the angle I_1-I_2 was 180° or very nearly so, and even when the anodic flank of I_1 towards which its bud deviated was equal to the other flank or even longer, instead of being the shorter as it normally is (see table 3). The eccentricities of buds will be discussed in §10.

The shape of I_1 in these apices, when it was a single leaf, is also of some interest, as its half over the wound, which was always the anodic half in relation to the direction of the spiral from P_1 to I_1 , usually covered a considerably larger arc than a normal anodic half (table 3, column 8). Indeed, in one apex, no. 84 (figure 18), it covered 201° . On the other hand, when the centre or anodic flank of P_1 was removed, then, as already pointed out, the half of I_1 , which was over the wound or was the closer to it, usually covered a *smaller* arc than the corresponding half of a normal leaf, but was thickened radially (table 2, and Snow, M. 1951, table 3). That half was the cathodic half except in nos. 290 and 294 of table 2, and its decrease is shown by the corresponding increase of the

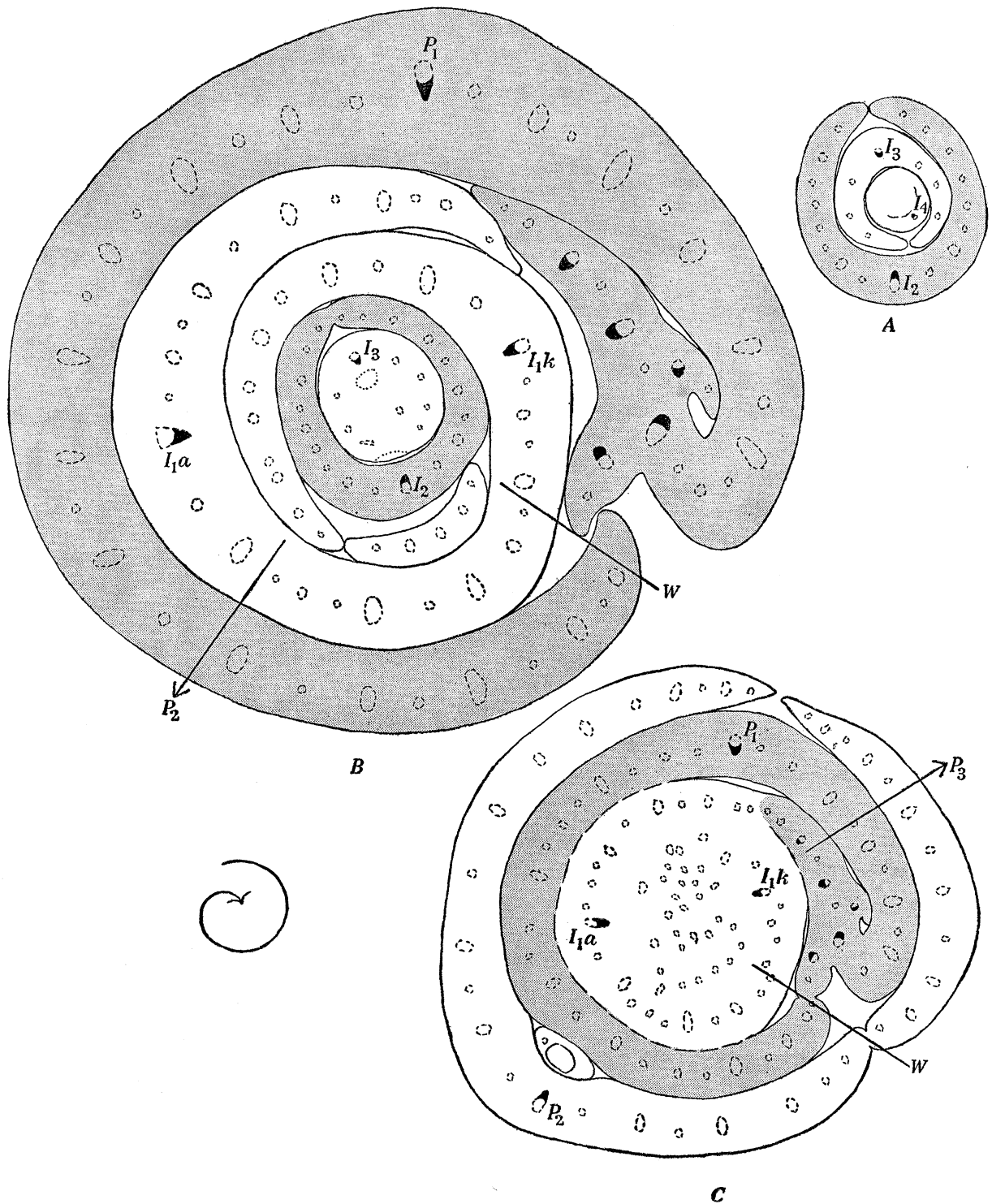


FIGURE 19. *A*, *B* and *C* are transections through apex no. 120. The presumptive area of I_1 was divided radially with a cut. I_1 was double, having a cathodic centre (I_{1k}) and an anodic centre (I_{1a}). The tip of the anodic flank of P_1 has developed abnormally, the xylem regions of its vascular strands are shown black. (Magn. *A* and *B*, $\times 36$; *C*, $\times 14$.)

anodic half recorded in the table. In nos. 290 and 294 also the half of I_1 over the wound was abnormally short, but was in these two the anodic half. So it appears that the removals of leaf centres or flanks regularly decreased the extension of the flank of I_1 above the wound, but the radial cuts increased it. This difference can be understood on the basis of the explanations already suggested, since when leaf centres or flanks were removed, the cuts, which were at right angles to the radii through their centres, displaced the growing-point away from them by increasing the radial growth of the apex above them. Correspondingly, these cuts increased also the thickness of the leaf flanks above them, and this in turn, as suggested above, decreased the peripheral extensions of the flanks. But when I_1 was divided by a radial cut, the cut seems not to have displaced the growing-point away, as has been pointed out. Instead the cut must have been something of an obstacle over which the flank of I_1 had to rise, and this would tend to make it thinner, and consequently longer, according to the rule suggested.

The later developments in these apices were not of special interest. The angle I_1-I_2 was usually larger than normal, but this can readily be interpreted either on the basis of a space-filling theory, or on that of physiological repulsions. For the centre of I_1 was closer than normal to the centre of P_1 , on one side of it or the other, so that I_2 was able to arise more nearly opposite to I_1 without coming unduly close to the centre of P_1 . The phyllotaxis then gradually returned towards the normal. In the last two apices, nos. 120 and 121 (figures 19, 20), I_1 was a double leaf having one morphological centre and axillary bud on each side of the cut, and a uniting region above the cut. In no. 120 (figure 19) the phyllotaxis is not instructive, since it was complicated by a remarkable turning in and development of the anodic flank of P_1 . But this turning in of the flank is itself of some interest and was probably due to the fact that in this apex alone the edge of the extending flank of P_1 at the time of operation had exactly reached the position where the cut was made, as was noted at the time. Consequently the flank then extended inwards along the radial cut, and finally broke up and extended in several directions, including the reverse direction round the apex, as the drawing indicates. It is of interest that in the reversed part the orientation of the bundles, in which the xylem is shown black, is not reversed, but is normal in relation to the axis. Yet it is difficult to regard this part as another leaf with which the flank of P_1 has united back to back, since it is too small. Other peculiarities are that the flanks of the double I_1 overlap instead of meeting and uniting, and that the extreme marginal part of its cathodic flank has developed separately except at its extreme base. Most of the cathodic part of the double I_1 was inserted at a higher level than the anodic part.

In no. 121 (figure 20) the two parts of I_1 were inserted at the same level. The subsequent phyllotaxis can be interpreted without difficulty. The spiral was reversed.

7. THE PHYLLOTAXIS OF THE AXILLARY BUDS

The development of the phyllotaxis in axillary buds and seedlings serves to test some of the interpretations suggested in the previous sections. Each axillary bud starts with a dorsal two-keeled prophyll of the kind usual in monocotyledons, having one main strand to each keel (see figures 21, 22). The two strands are roughly in the transverse positions, and one of them is marked as the true morphological centre by subtending an axillary

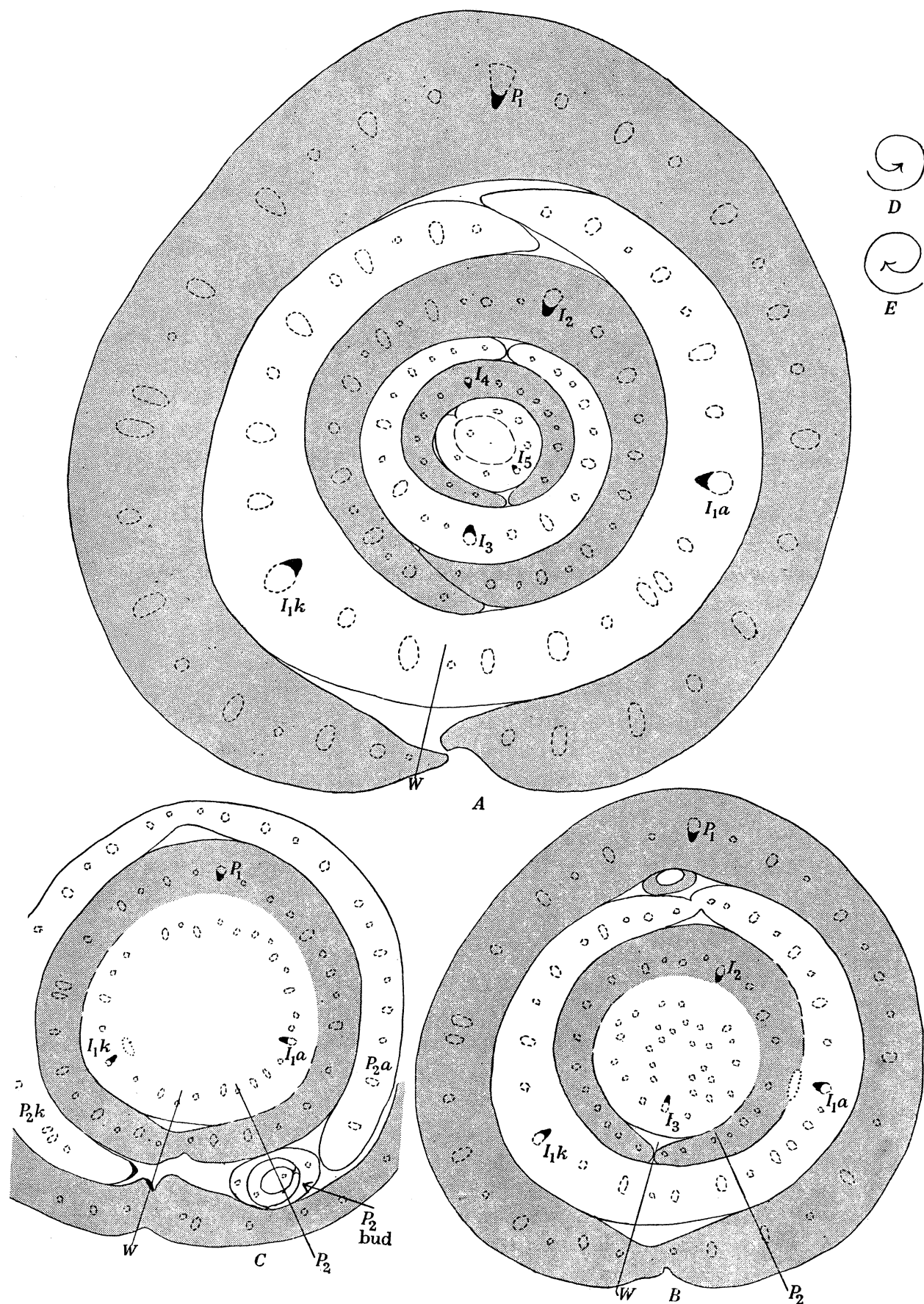


FIGURE 20. A, B and C are transections of apex no. 121. The presumptive area of I_1 was divided radially with a cut. I_1 was double, having a cathodic centre (I_{1k}) and an anodic centre (I_{1a}). (Magn. A, $\times 37$; B, $\times 24$; C, $\times 14$.)

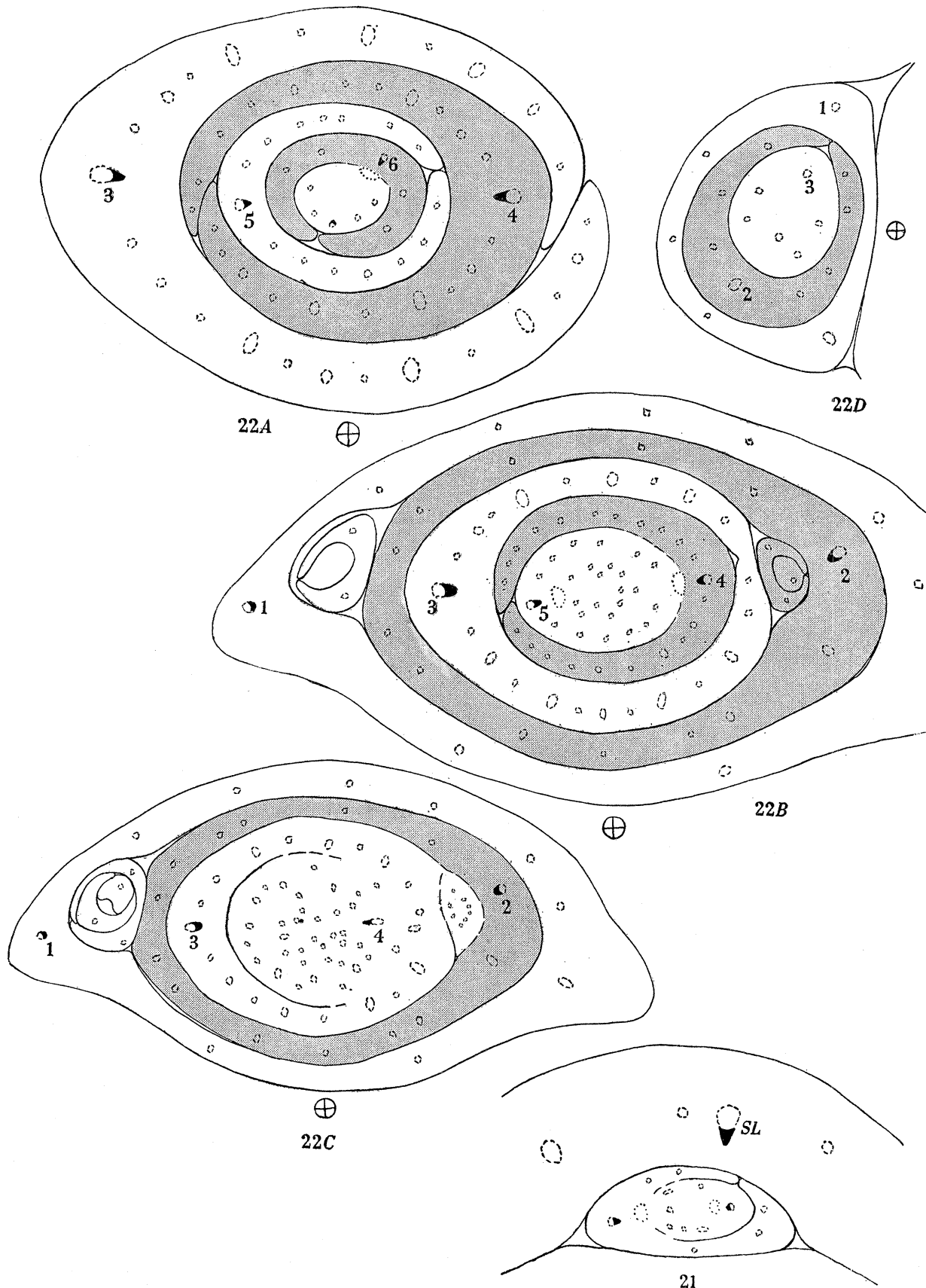


FIGURE 21. Transection of a young axillary bud and of the central part of the subtending leaf, *SL*. (Magn. $\times 85$.)

FIGURE 22. *A*, *B* and *C* are transections of axillary bud no. 5. *D* is a transection of the axillary bud of its prophyll. In this and subsequent drawings of axillary buds the prophyll is numbered as leaf 1. The main axis is marked with a cross in a circle. (Magn. *A*, $\times 43$; *B*, $\times 33$; *C*, $\times 16$; *D*, $\times 65$.)

bud. This agrees with a rule stated by Arber (1925, p. 135), on the basis of observations made by Rüter (1918) for monocotyledons generally. The morphological centre can also be seen to arise before the rest of the prophyll, and it is regularly at the anodic side of the bud. This is clearly the side on which there is the more room for formation of a leaf centre, since the whole bud is eccentric in the anodic direction. Weisse (1889) has described and interpreted the shape of the prophyll and the position of its morphological centre in some other monocotyledons in a similar way, except that he states his interpretation in terms of least pressure instead of greatest available space.

The prophyll will be called leaf 1 of the bud, and the divergence angles from it are measured from its morphological centre. Leaf 2 is very roughly opposite to the morphological centre of leaf 1 (see table 4), and thus roughly in a transverse position also. Leaves 1 and 2 are long sheaths with little or no expanded blade, and the morphologically central parts of their bases are scarcely thicker than the lateral parts, unlike the central parts of the foliage leaves. The subsequent leaves continue roughly transversely distichous up to leaf 5 inclusive, or in the last two of the nine buds recorded in the table, up to leaf 4 only; but they tend to converge a little towards the subtending leaf. For the angles recorded in table 4, up to leaf 5 or leaf 4, are all measured on the side towards the subtending leaf and are mostly below 180° , though not very far from it. The next angle, however, the angle 5-6 or 4-5, is smaller, usually much smaller, and sometimes even less than the mean normal angle of 152.6° . So the leaf to which it leads deviates conspicuously from the previous transverse distichy, and this leaf, the first deviating leaf as it may be called, starts a spirodistichous phyllotaxis which continues. The distichous leaves mostly have their peripherally shorter halves towards the subtending leaf. The first leaf of the spiral sequence may be on either side of the bud.

TABLE 4. AXILLARY BUDS.

All measurements in degrees.

numbers of buds	angles between successive leaves measured on side towards subtending leaf				divergence angles of leaves in spiral sequence		arcs of the leaf halves nearer to the subtending leaf				arc of anodic half of leaf
	1-2	2-3	3-4	4-5	5-6	6-7	2	3	4	5	6
1	187	179	182	178	135	159	—	178	171	185	179
2	180	168	180	180	151	—	—	171	171	175	178
3	177	181	181	174	—	—	173	171	180	171	—
4	173	164	171	166	161	140	162	163	161	172	177
5	174	172	177	187 173}	142	151	175	167	184	170	166
6	171	167	182	185	152	137	—	—	180	166	174
7	163	173	173	189 171}	139	145	—	175	180	162	167
				divergence angles of leaves in spiral sequence							arc of anodic half of leaf
8	163	180	198 162}	150	144	—	—	180	180	170	—
9	176	166	179	139	147	153	165	171	175	172	—

Note. The first leaf of the spiral sequence was situated on the side of the bud towards the subtending leaf in nos. 5, 7 and 8 and towards the axis in the others. Thus it was in the larger angle between the two previous leaves except in no. 6. In the distichous region, where a divergence angle measured above the subtending leaf considerably exceeded 180° , the supplementary angle is bracketed with it.

The first question which arises is how it is that the first five or four leaves are roughly distichous. In the first place the morphologically central parts of leaves 1 and 2 are thin and do not form any well-marked hump; so they would not be expected to cause subsequent leaves to deviate into spirodistichy, as do the centres of normal leaves according to the suggestion made in § 3. But even so leaf 5 might be caused to deviate by the central part of leaf 3, whereas actually in the first seven buds measured leaf 6 was the first to

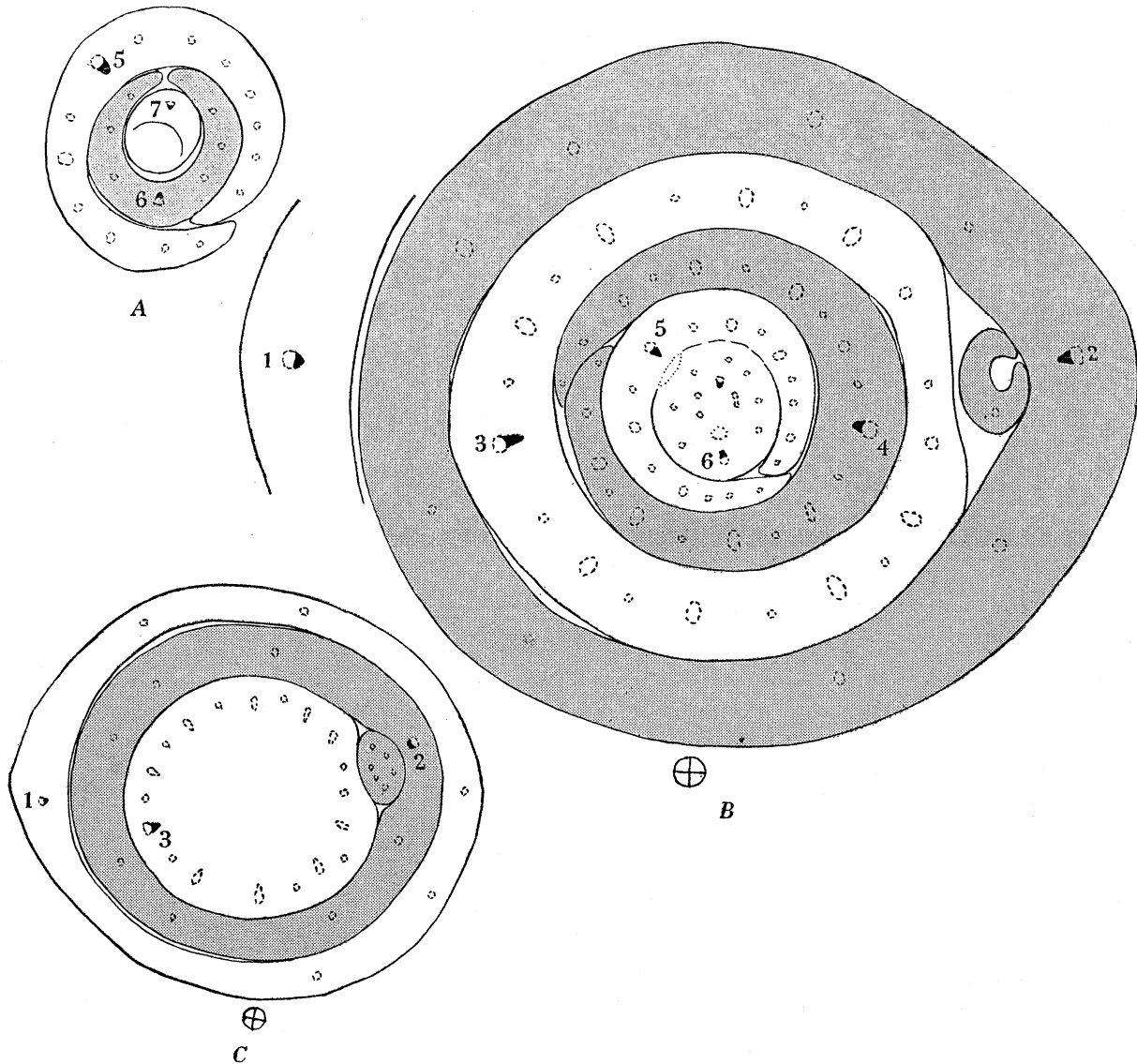


FIGURE 23. *A*, *B* and *C* are transections of axillary bud no. 8. (Magn. *A*, $\times 42$; *B*, $\times 36$; *C*, $\times 16$.)

deviate. So some other factor must be at work in keeping the phyllotaxis distichous, and it is here suggested that this is the shape of the stem apex of the young bud, which can regularly be seen to be elliptic and extended in the transverse direction (see figure 21). For it is known that in many species, though not in all, the leaves tend to arise with their centres at the narrow ends of an elliptic stem apex, which are the positions farthest from the summit of the apex. The elliptic shapes of the apices of the young axillary buds are probably due in turn to a compression of the stems of the buds, just below their apical

cones, between the subtending leaf and the main axis; for the apices of older axillary buds and outgrown shoots of *Rhoeo* are not elliptic. It agrees with this interpretation that in the two buds which became spiral sooner than the others, nos. 8 and 9 of table 4, the stem apices were perceptibly less elliptic (figure 23, no. 8). Moreover, in no. 8 the prophyll has no well-marked keel, which also suggests that the usual pressure was lacking.

The fact that in the nearly distichous region the leaves of the bud mostly converge a little towards the subtending leaf is probably to be explained as follows. In longisections of young axillary buds, having only three leaves or less (figures 24, 25 and 26) it can be seen that the apex of the bud grows up nearly vertical, and that the distance from the summit of the bud apex to the youngest leaf encircling it is greater on the side towards the subtending leaf. On a space-filling theory, therefore, the centres of subsequent leaves will be displaced towards this side. Similarly, the directions of growth of the axillary buds in various species were considered by Schwendener (1878, p. 98) and Weisse (1889) to be critical for the positions of certain of their leaves. In a bud having five leaves, the apex as seen in longisection is much less asymmetric (figure 27).

It may also be expected that the halves of the distichous leaves on the side towards the subtending leaf, where there is more room on the bud apex, will be radially the thicker, and this, according to the rule noted in the previous sections, will tend to make them peripherally the shorter, as they were mostly found to be (table 4).

The suggestion that the compression of the young axillary buds, by extending their apices transversely, keeps them roughly distichous in the transverse plane up to leaf 5 is further supported by an experiment in which a fine glass needle was inserted into the stem of a main apical bud just internally to the bud meristem of the axillary bud of P_3 . The needle was moved about a little, so that it made a cavity in the main stem into which the axillary bud was able to expand (see figure 28), instead of being compressed between stem and subtending leaf. Later when pickled the axillary bud was found to have formed four leaves, of which leaves 2, 3 and 4 were roughly distichous, but in the median plane, as can be seen in figure 28. Leaf 1, the prophyll, showed an injury next to the cavity. That the leaves 2, 3 and 4 of this bud were roughly distichous can be understood, since the centre of leaf 3 did not come over any central hump in leaf 1, nor did the centre of leaf 4 come over any well-marked central hump in leaf 2; for leaf 2 of an axillary bud has a thin central part, as already mentioned. The median distichy can be attributed to the fact that the bud was not compressed nor its stem apex extended transversely in the usual way.

Buds with median distichy are also sometimes formed naturally in *Rhoeo*. The writer has found five such buds amongst a large number observed. Three of these were secondary buds, two being in the axils of the first leaves or prophylls of primary axillary buds (see figure 29) and one in the axil of the second leaf. In the last of these the plane of distichy was slightly oblique (figure 30). The morphological centres of these first two leaves would not be expected to compress their secondary axillary buds so much as later leaves, both because these two leaves are thin and weak and also because their blades on each side of the morphological centre are compressed in the direction at right angles, together with the whole primary axillary bud, between the leaf subtending that bud and the main stem (see figure 22*B, C*).



FIGURES 24, 25, 26 and 27 are longisections of axillary buds nos. 10, 11, 12 and 13, together with parts of the main axes. The main axes are all vertical in the drawings. In these and other sections of axillary buds the subtending leaves are marked *SL* and the leaves next above them on the main axes are marked *L₂*. The arrow *Ax* points to the centre of the main axis. Figure 27*B* shows the apical region of figure 27*A* more highly magnified. (Magn. 24, × 86; 25, × 88; 26, × 82; 27*A*, × 65; 27*B*, × 106.)

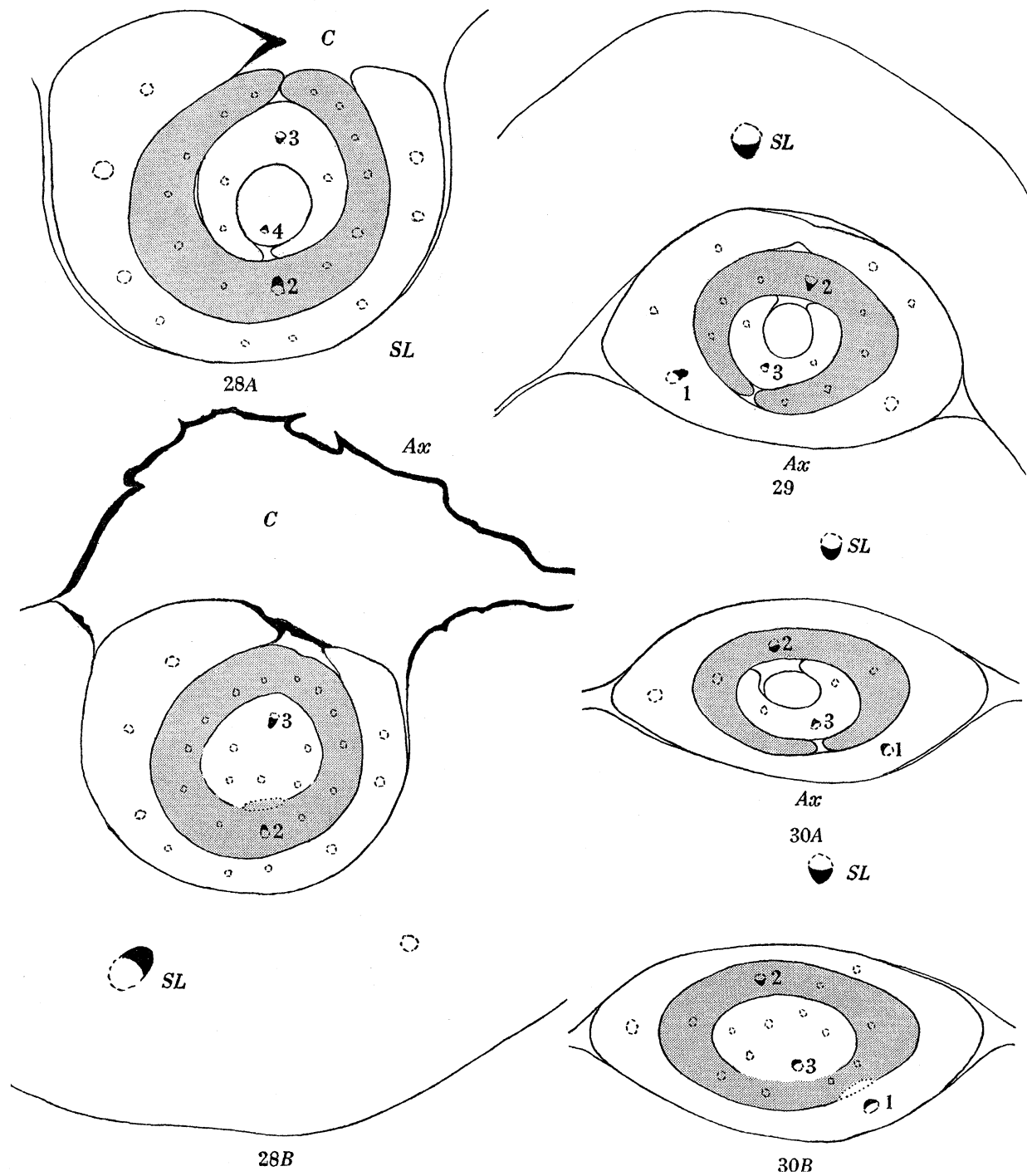


FIGURE 28. *A* and *B* are transections of an abnormal axillary bud with median distichy. A cavity *C* was made with a needle in the tissues of the axis next to the bud. The prophyll was injured and has no median strand. The axis is marked *Ax*. (Magn. *A*, $\times 73$; *B*, $\times 58$.)

FIGURE 29. Transection of an abnormal bud in the axil of a prophyll. It has median distichy from leaf 2 onwards. (Magn. $\times 54$.)

FIGURE 30. *A* and *B* are transections of an abnormal bud in the axil of the second leaf of an axillary bud. The bud is approximately distichous in an oblique plane. (Magn. *A*, *B*, $\times 58$.)

Each of the other two buds with median distichy was in the axil of the first leaf of a seedling, and was nearly median in this axil. It is not yet known whether the buds in this axil are regularly like this.

8. THE PHYLLOTAXIS OF THE SEEDLINGS

In the seedlings, which have apices that are not compressed and flattened like those of the axillary buds, the phyllotaxis becomes spiral much sooner, usually at leaf 2, the second leaf after the cotyledon. For the divergence angle from leaf 1 to leaf 2 is considerably less than 180° , though very variable, and a spiral sequence continues in the same direction from leaf 2 onwards (see table 5 and figures 31, 32). So here the special problem is how it is that leaf 2 is not opposite to leaf 1, since from leaf 3 onwards the phyllotaxis can be interpreted in the way suggested in §3.

TABLE 5. YOUNG SEEDLINGS

All measurements in degrees.

numbers of apices	divergence angles			arcs subtended by anodic halves of leaves	
	1-2	2-3	3-4	1	2
1	149	155	133	—	184
2	151	172	136	—	193
3	166	133	—	177	180
4	164	125	149	—	187
5	160	140	—	180	187
6	132	—	—	180	182
7	173	106	—	170	178
8	128	119	170	174	175
9	171	186	—	171	180
		174			

The cotyledon is tubular, and the centre of leaf 1 is stated by Hirmer (1922, p. 42) to be in the median plane of the cotyledon, a plane which, to judge from his figure 36, he takes to be at right angles to a plane including two opposite strands of the cotyledon. But the writer finds that the two strands of the cotyledon are usually not quite opposite, and the centre of leaf 1 is usually not midway between them (see figures 31, 32). Also in one seedling (no. 2 of table 5) the cotyledon had three strands. Indeed, a median plane or morphological centre of the cotyledon could not be located, since the cotyledon was not seen to have an axillary bud, and its reflexed tip, which remains in the seed as a haustorium, was found at various angular positions in relation to the strands of the tubular region nearer to the base, and also in relation to leaf 1.

A clue to explaining the position of leaf 2 may be that the anodic half of leaf 1 was usually found to be the shorter peripherally, when the junction of the flanks could be located, and so also was usually the cathodic half of leaf 2 above it (see table 5, in which the arcs of the anodic halves of both leaves are recorded). Thus the shorter half of leaf 1, and usually that of leaf 2, was on the side of the apex towards which the centres of these leaves converged. This agrees with the rule that a side of the apex favourable for the formation of leaf centres is unfavourable for the extension of leaf flanks, and it suggests that different sides of the apex have been subjected to different conditions in the seed before germination.

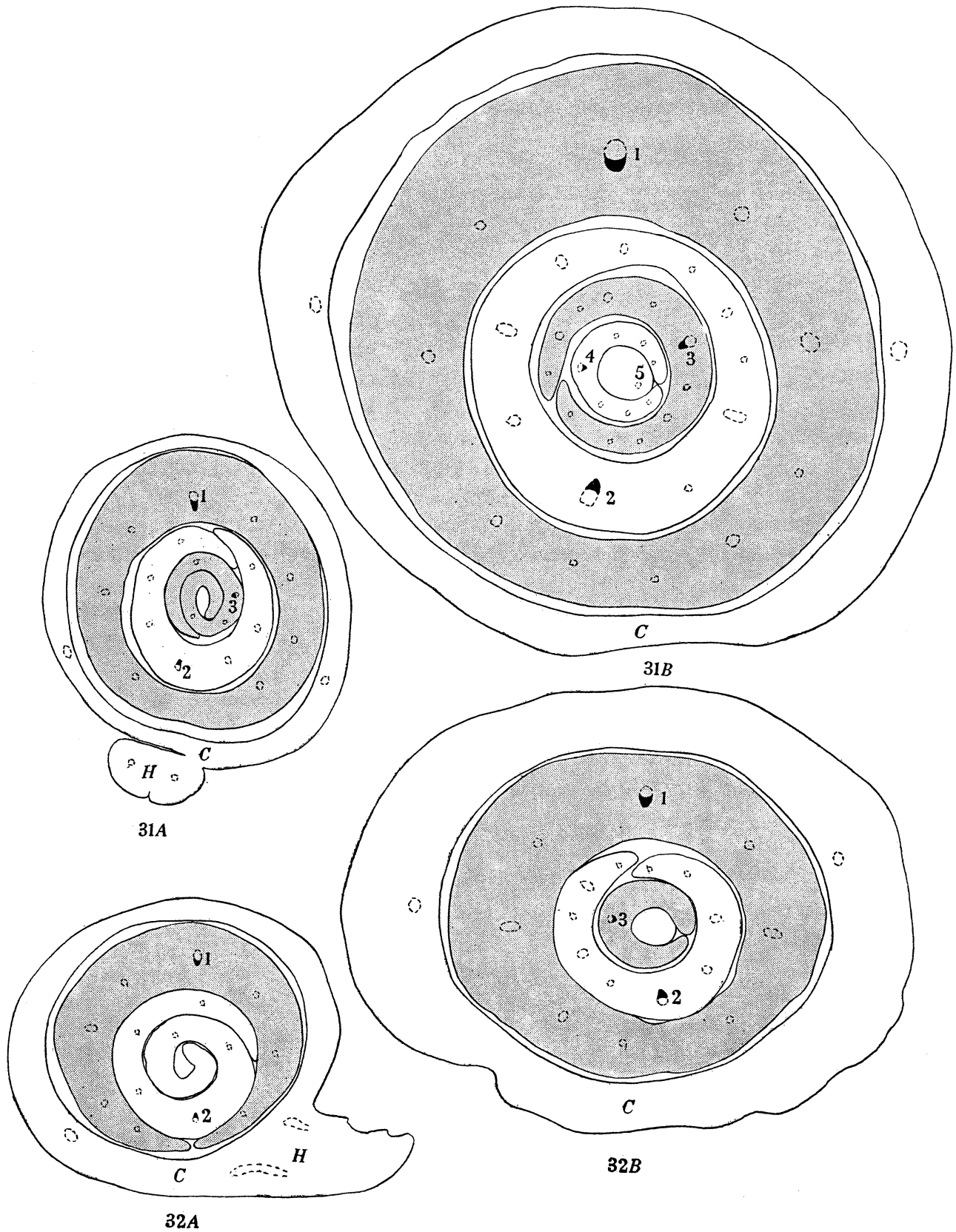


FIGURE 31A, B and FIGURE 32A, B. Transections of seedlings nos. 4 and 7. *C* is the cotyledon and *H* its haustorium. (Magn. 31A, $\times 21$; 31B, $\times 44$; 32A, $\times 32$; 32B, $\times 53$.)

9. LEAF ASYMMETRY

The normal asymmetries of the leaves were described previously (Snow, M. 1951, pp. 134, 139). The flanks of each new leaf extend round the apex, and they meet and unite at their bases before the next leaf arises. The anodic half of each leaf, from its morphologically central strand to the junction of its flanks, was found to cover a mean arc of 166.5° ; but this half, though the shorter peripherally, was the thicker radially. Observations are needed on other spirodistichous species to show whether their leaf asymmetry is similar.

In the experiments reported here and previously (Snow, M. 1951), the asymmetries of I_1 and I_2 were often abnormal, but very frequently the peripherally shorter half of the leaf was the thicker radially, as in the normal. Moreover, it was shown in §4 that the radial thickening was probably due to an increased radial growth of the stem apex above the wound, associated with a shift of the growing-point away from the wound. It seems therefore that the causal connexion was that the radial thickening of one half of a leaf caused it to be the shorter peripherally, perhaps by using up in a different way something necessary for growth, as was suggested above; for it seems unlikely that the increased radial growth of the stem apex above the wound altered directly the peripheral extension of the leaf flank in that region, but very likely that it increased the radial thickness of that flank.

The question therefore arises whether in the normal apex also the unequal peripheral extensions of the halves of a leaf are due to their unequal radial thicknesses, and, if so, what makes them unequally thick. In answer to this question, a suggestion will here be made which may at first seem rather complicated, but will be supported by further evidence from the experiments. First it must be recalled that in *Rhoeo* the leaf flanks, as was pointed out in §3, develop gradually and independently, and adjust themselves to their situations. Thus their bases were seen to grow closer to the summit of the apex in passing over the obstacle of a radial cut, as was pointed out; and where they did so they were sometimes seen to become thinner, for instance in apex no. 84 (figure 18, p. 68). They also become radially thicker in occupying the region above a tangential wound, which seems to be enlarged radially (§§2, 4). Accordingly, it is now suggested that in a normal *Rhoeo* apex the anodic half of each leaf is made radially thicker by occupying the slight depression above the junction of the flanks of the previous leaf (see figure 1), and is thereby made shorter in peripheral extension. It is also suggested that the cathodic flank is made radially thinner by growing closer to the summit of the apex where it passes over the central part of the previous leaf and over its bud area, and that thereby it is made peripherally longer. It may be recalled that this rising up of the cathodic flank of a leaf over the centre of the previous leaf is also the factor which, according to the suggestion made in §3, makes the phyllotaxis spirodistichous.

This explanation of the normal leaf asymmetry is strongly supported by the results of the experiments. For it has been found possible to explain on the same basis the shapes of the I_3 leaves, which had previously been found very puzzling, as well as the shapes of certain leaves in normal axillary buds. It was not indeed surprising that the I_2 leaves in the experiments were more nearly symmetric than normal leaves, as was pointed out previously (Snow, M. 1951, p. 156), and as was found again in the present experiments;

for the angle I_1-I_2 was usually much increased, so that the I_2 's were brought more nearly opposite to the I_1 's. But it was at first very surprising that the I_3 's also were often nearly or quite symmetric (see tables 2, 3), although the angle I_2-I_3 was usually less than the normal, its mean value in the relevant apices, those discussed below and included in figure 33, being only 141.5° . So I_4 was the first leaf that was normally asymmetric, at least when it was large enough to be measured, although the spiral phyllotaxis was fully re-established at I_3 .

The frequent approach to symmetry of I_3 cannot have been due to a thickening and shortening of its flank above the wound, such as was often seen in I_1 and I_2 . For the flank of I_3 above the wound might be either flank, and except in one apex it was not noticeably thickened, presumably because usually the shift of the growing-point was nearly finished when I_3 was arising. It therefore seemed that the explanation must be sought in the varying shapes of I_1 and I_2 and in the varying position of their centres and of their other parts in relation to each other and to I_3 . So a number of such variables were measured and plotted in graphs against the approach to symmetry of I_3 , as indicated by the arc covered by its anodic half. The apices on which the measurements were made were not only those reported here and previously, in which P_1 or I_1 was operated upon, but also twenty-six other apices regenerated from the halves formed by splitting apices in a median plane at right angles to the median plane through the centre of P_1 . The earlier developments of these apices were rather various and complicated, but their I_3 's were similar in shape to those in the other apices and seem quite comparable, since the angle I_1-I_2 was often large.

One of the variables plotted was the angular distance from the junction of the flanks of I_2 to the centre of I_1 , a distance which was less than the normal 41° in nearly all these apices, since it was diminished both by the increase of the angle I_1-I_2 , and by the increase of the anodic half arc of I_2 (see figure 9). It was with this variable that the arc of the anodic half of I_3 was found to be most closely correlated—more closely than with the angle I_1-I_2 . The correlation, which was inverse and is shown graphically in figure 33 makes it appear that the smaller the distance from junction of flanks of I_2 to the centre of I_1 , the larger was the arc of the anodic half of I_3 , and so the closer the approach of I_3 to symmetry.

It can be seen that forty-five apices follow fairly closely a line showing an inverse correlation between the variables, and tending to a limit of 180° for the anodic half of I_3 (abscissae), where the other variable falls to 15° or less. In four other apices the anodic half of I_3 is distinctly too short to conform, and in four it is distinctly too long. Most of the eight exceptional apices appeared as exceptions in the other graphs also, so that probably they were influenced by some exceptional undetected factors.

It can hardly be doubted that the inverse correlation shown in the graph is genuine, and it can be readily explained in accordance with the suggestions made above that normally the anodic half of each new leaf is thickened, and thereby shortened, in occupying the depression above the junction of the flanks of the previous leaf. For in the experiments the junction of the flanks of the previous leaf, I_2 , was often closer to the centre of I_1 than the normal distance of 41° (see, for example, figure 9, no. 265, and figure 18, no. 84); and the closer the junction of the I_2 flanks was to the centre of I_1 the more it was raised up

towards the summit of the apex; and thereby the depression above it was made less effective in thickening and shortening the anodic flank of I_3 above.

The question remains whether in these I_3 leaves there was also a diminution of the other factor which, according to the suggestion made above, contributes to making a normal leaf asymmetric—a diminution, that is, of the thinning out and lengthening of its cathodic flank above the central part of the previous leaf. It does seem that this factor also, the cathodic factor as it may be called, must have been greatly diminished or absent in many of the I_3 leaves, since nine of them were exactly symmetric, and one was even

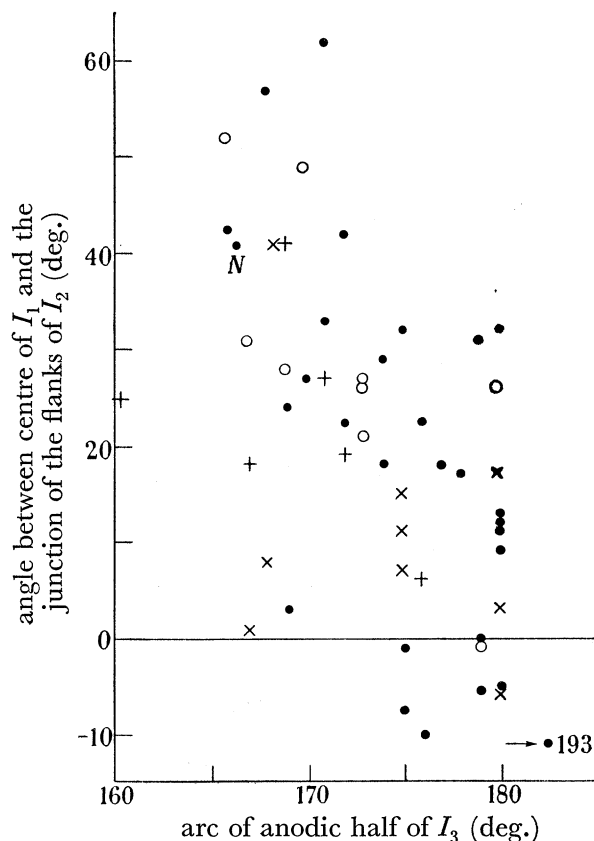


FIGURE 33. Graph showing relation between the arc covered by the anodic half of I_3 (abscissae) and the angle from the centre of I_1 to the junction of the flanks of I_2 (ordinates) in apices operated upon in four ways distinguished by symbols as follows: \times centre of P_1 removed. \circ anodic flank of P_1 removed. $+$ presumptive area of I_1 divided radially. \bullet apices regenerated from the halves of apices split in a median plane. The point N shows the mean normal value. On the ordinates the cathodic direction is shown as positive and the anodic as negative.

asymmetric the other way. Such a diminution of the cathodic factor would be expected to result from the observed increases of the angle I_1-I_2 for the following reason. According to the suggestion made in § 3, the mean divergence angle (152.6°) between two successive leaves $n-1$ and n is less than it otherwise would be, because the younger leaf, n , is displaced laterally by the rising up of the cathodic flank of leaf $n-1$ over the central part of leaf $n-2$. Since therefore in the experiments the angle I_1-I_2 was usually much increased, it may be inferred, on the basis of this suggestion, that I_2 was usually not displaced laterally so much

as is normal by any rising up of the cathodic flank of I_1 . So I_2 must have occupied a lower position in relation to the previous leaf (I_1) than is normally available. Consequently the central part of I_2 would not be expected to cause the cathodic flank of I_3 to rise up so much as is normal in passing over it. That flank, therefore, would not be so much thinned out radially nor so much lengthened peripherally.

An approach to symmetry in a similar situation is shown by the leaf which in the axillary buds is the first to deviate from distichy into spirodistichy. This leaf, to be called leaf n , was the sixth leaf in the first seven apices of table 4, and the fifth in the last two. The situation of leaf n was similar to that of the I_3 's in the experiments, since the angle from $n-1$ to n had a mean value of only 146.1° (table 4), whereas the previous angle was much larger, its mean being 174.2° . In the two buds of table 4 which became spiral more gradually (nos. 4 and 8), leaf n was taken to be the first leaf which diverged by more than 30° from the previous leaf but one.

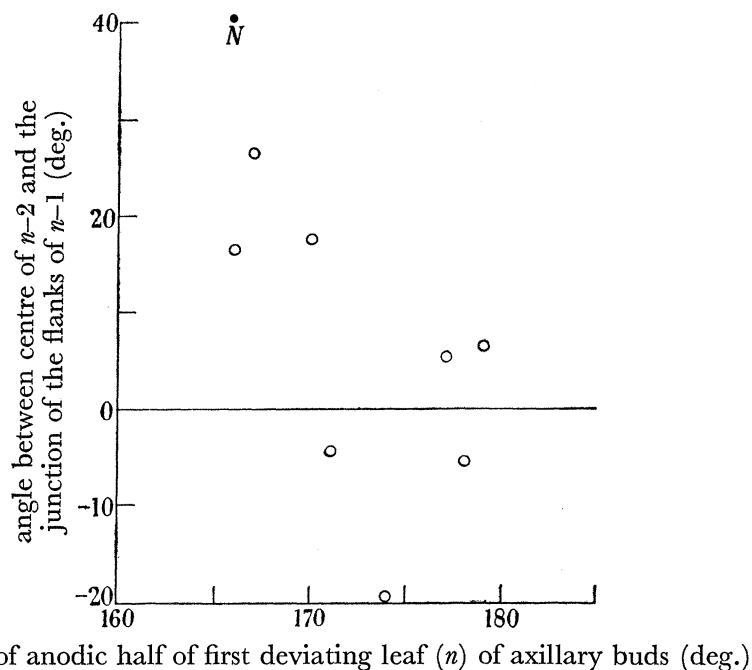


FIGURE 34. Graph showing relation between the arc covered by anodic half of first deviating leaf, called n (abscissae), and the angle from the centre of leaf $n-2$ to the junction of the flanks of leaf $n-1$ (ordinates) in axillary buds. The point N shows the mean normal value in apical buds of mature shoots. The cathodic direction is shown as positive.

The table shows that leaf n , as well as leaf $n-1$, was more nearly symmetric than the normal, just as was I_3 as well as I_2 in the experiments. Also the corresponding graph (figure 34) shows similarly that the arc of the anodic half of leaf n is inversely correlated with the angular distance from the centre of $n-2$ to the junction of the flanks of $n-1$, which distances are all considerably less than the normal 41° . So this supports the explanation of leaf asymmetry suggested above.

Another leaf which was very nearly symmetric in a similar situation was I_4 in apex no. 121 (table 3 and figure 20), an apex made peculiar by having a double I_1 . For the angle I_3-I_4 was only 143° , but the anodic half of I_4 covered an arc of 179° . The angle from

the centre of I_2 to the junction of the flanks of I_3 was only 12° instead of the normal 41° , which again supports the explanation suggested.

I_3 , also in this apex and in the other apex with a double I_1 , no. 120 of table 3, figure 19, was very nearly symmetric, its anodic half covering an arc of 180° or 179° . But this seems to have been due to a different cause, that the centre of I_3 in these two apices was nearly or exactly in the depression above the junction of the flanks of I_2 , so that I_3 was not made asymmetric by having that depression under one flank. Also since the angles I_2 - I_3 were rather large, 168° and 165° , the cathodic flank of I_3 was not appreciably extended in passing over the centre of I_2 ; for it met and was stopped by the other flank only a very little way beyond that centre (see figures 19 and 20).

10. BUD ECCENTRICITY

The normal axillary bud of *Rhoeo* is eccentric, being on the anodic side of the median strand of the subtending leaf, as was mentioned previously (Snow, M. 1951, p. 136). The eccentricity is about 5° when the bud first becomes a definite hump, as it does in the axil of the fifth or sixth leaf. But the first indication of the coming bud is a dark merismatic patch in the axil of the second leaf, and this patch, which is thin radially but much more extended tangentially, is median so far as the eye can judge. The actual bud arises up later from the anodic end of the merismatic patch. After some of the operations the position of the bud of P_2 , P_1 or I_1 could be seen and was of some interest. When the anodic flank of P_1 was removed, the bud of P_1 was regularly much more eccentric than the normal, its mean eccentricity in ten of these apices being 15.4° (table 2). Also in four of these apices the bud of P_2 was only 2° eccentric or less. Thus both these buds were displaced towards the cut. These changes may possibly have been due to the fact that the cut which removed the anodic flank of P_1 also isolated P_3 below it from the rest of the apex. But rather unexpectedly the removal of the central part of P_2 never displaced the bud of P_1 .

When the presumptive area of I_1 was divided radially, I_1 might arise on either side of P_1 , but the bud of I_1 (when I_1 was a single leaf) was always anodic from P_1 , as reported in §6. After the other operations the position of the bud of I_1 might have been instructive, but usually it had not developed far enough for its final position to be seen clearly. Further experiments are needed designed for the purpose of revealing what makes the buds eccentric.

11. CONCLUDING REMARKS

It has been shown that the changes of leaf position after the previous operations on *Rhoeo* (Snow, M. 1951) and after others reported here can be explained on a space-filling theory after all, if the shift of the growing-point is taken into account, as unfortunately was not done previously. Also it has been pointed out that the normal spirodistichy of *Rhoeo* can be interpreted on a space-filling theory, since the bases of the leaf flanks in *Rhoeo* extend independently round the apex and rise up towards the summit of the apex where they pass over the obstacle of an underlying leaf centre, so that they modify in turn the space available for the next younger leaf. In this way one leaf can affect the position of the next younger leaf but one, although their bases are not in contact; and it is not necessary to suppose that one leaf physiologically inhibits or repels the position in which a younger leaf is determined, as the writer supposed previously. Moreover, the theory of

physiological repulsions has been shown to conflict with the results of some of the operations reported here (§2). This removes what had previously seemed to be a big and surprising way in which monocotyledons differed from dicotyledons; for in the latter there were found to be no such physiological repulsions (Snow & Snow 1952, p. 560). Also evidence has been given in §6 that in *Rhoeo*, as in dicotyledons, there is a minimum primary arc on which a leaf can be determined, though this arc is much smaller in relation to the arc finally covered by the leaf base, and more difficult to estimate. The clearest evidence supporting the space-filling interpretations here proposed is provided by the results of the experiments reported and discussed in §6 (see p. 66).

A process rather similar to the rising up of the leaf flanks of *Rhoeo* over an obstacle may take place in some dicotyledons, since according to R. Snow (1951) a process of this kind is one of two factors which make the phyllotaxis of teasels bijugate or doubly spiral instead of decussate. For he considers that the thin zone uniting the bases of the leaves of each pair approach closer to the apex in passing over the central parts of the next older pair of leaves, and thereby displace sideways the leaves of the next younger pair. Similar processes may be at work in still other groups. They fall within a space-filling theory of phyllotaxis, but go beyond van Iterson's original space-filling theory (1907), which was expressly limited to plants in which the leaf bases are circular, or rather would be circular if the apical cone on which they are inserted were unrolled into a plane. For in the teasels if the zones uniting the leaves of a pair are considered as parts of the leaf bases, then the whole leaf bases are not circular.

The phyllotaxis of the axillary buds and seedlings has been discussed and interpreted in accordance with the space-filling theory proposed, the phyllotaxis of the axillary buds being apparently modified by their compression between subtending leaf and axis. It has also been found possible to propose, on the basis of evidence provided by the experiments, an explanation of the asymmetry of the leaf bases in *Rhoeo*, an asymmetry which is very characteristic of spirodistichous phyllotaxis. But the eccentricities of the axillary buds need special experiments to reveal their causes. Also needed are observations of other spirodistichous species, to find whether their phyllotaxis and leaf asymmetry follow the same rules as those of *Rhoeo*.

The plasticity of the leaf flanks in *Rhoeo* greatly complicates the results of experiments upon the apices. For when the local conditions are changed by operations, the young leaves change their shapes by changes in the growth of their flanks, and this modifies the positions of the centres of subsequent leaves. This peculiarity, in addition to the much greater technical difficulties of the operations, has made it much harder to reach an understanding of the phyllotaxis in *Rhoeo* than in the other species so far studied; for in other species operations on the apex lead to much simpler and more clear-cut changes in the positions of the subsequent leaves.

I should like to thank Dr F. A. L. Clowes for the photomicrograph of the stem apex, Mr G. W. Robinson, Superintendent of the Botanic Garden, Oxford, for raising the seedlings and cuttings, Mrs Beryl Froud for preparing the sections of the young normal seedlings, and my husband for advice and help throughout the course of the work, and particularly for help in presenting the results.

APPENDIX

The measurement of the ratios of the distances of successive leaves from the centre, or plastochron ratios used in figure 6

The distances from the centre of the axis to the median strands of leaves 2 to 6 in six or seven normal apices were measured in transverse sections made at the level of insertion of leaf 2. The ratios of the mean distances of successive leaves decreased in the manner shown graphically in figure 35, and in figure 6 lines having relative lengths agreeing with these mean ratios were taken to represent the distances at the end of a typical experiment to I_2 , I_1 , P_1 and P_2 . Usually in the experiments I_4 was the youngest leaf that arose, or some-

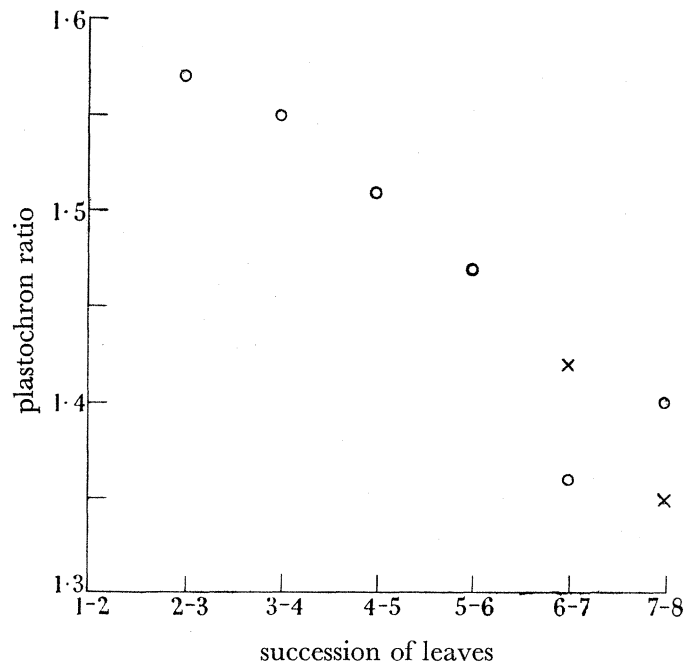


FIGURE 35.

times I_5 . The mean distances to leaves 7 and 8 measured similarly in five of these normal apices were rather aberrant, an excessive mean distance to leaf 8 being probably caused by the outgrowth of an axillary bud which pushed its blade outwards. So other values for the plastochron ratios of leaves 6 to 7 and 7 to 8 were estimated by continuing the curve and are shown by crosses; and were used in figure 6 to estimate the distances to P_3 and P_4 . The ratios of the measured values are shown as circles in figure 35.

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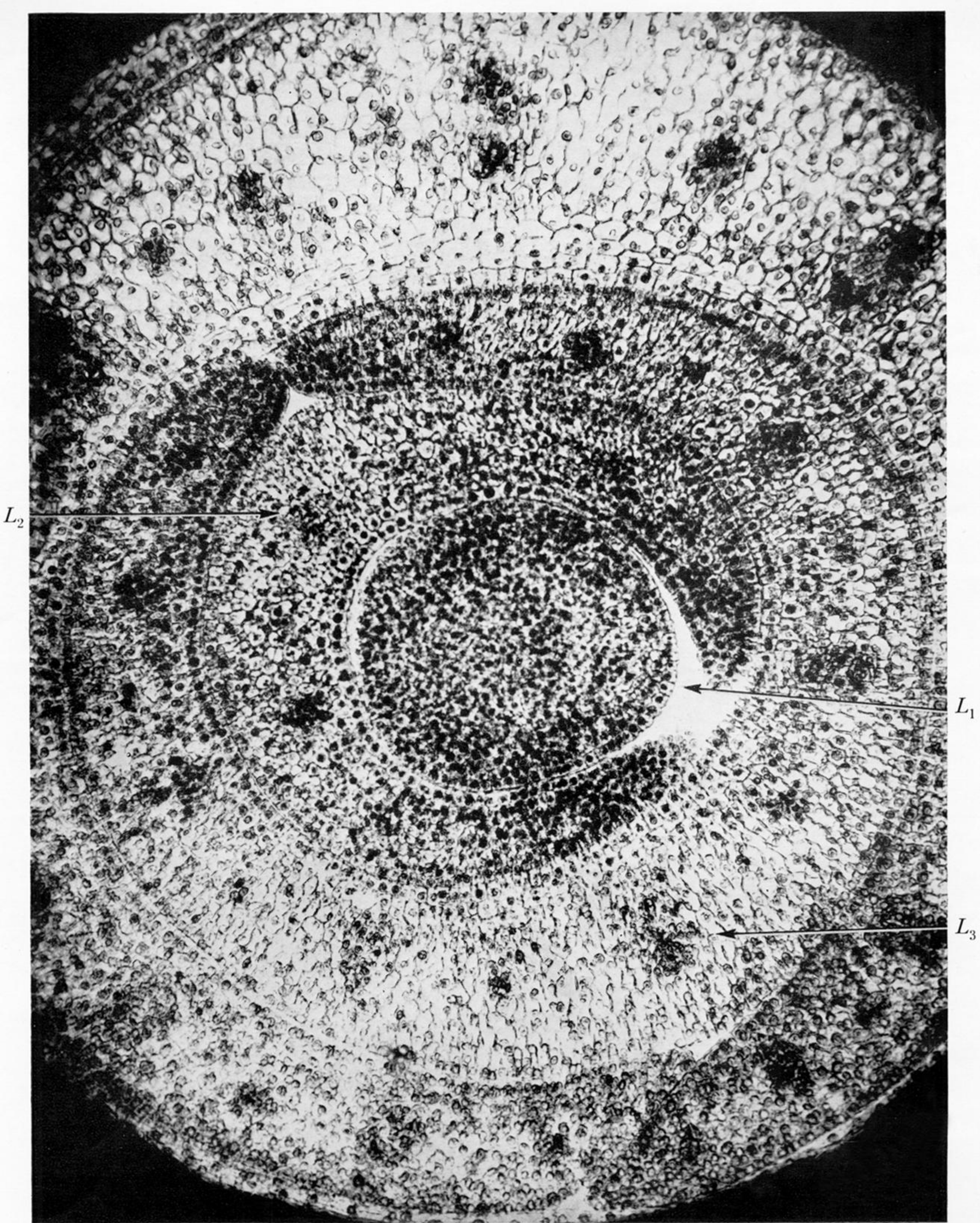


FIGURE 8. Photograph of a transection of a normal apex of *Rhoeo discolor* just above the insertion of the second youngest leaf. The genetic spiral wound clockwise. The arrows L_1 , L_2 and L_3 point to the centres of leaves one, two and three respectively. (Magn. $\times 152$.)