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Experiments on Phyllotaxis. Part III. Diagonal Splits through Decussate Apices

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II—Experiments on Phyllotaxis

Part III—Diagonal Splits through Decussate Apices

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CONTENTS

Page

I—INTRODUCTION . . . 63
  1—General . . . 63
  2—Materials and methods . . . 64
  3—The normal apex of *Epilobium hirsutum* . . . 65
  4—The nature of the operations and the resulting regeneration . . . 67
II—RESULTS OF EXPERIMENTS . . . 67
  5—Preliminary review of results . . . 67
  6—The spiral apices . . . 68
  7—The divergence angles in the spiral apices . . . 76
  8—The nearly decussate apices . . . 79
  9—The apices with I_3 and I_4 joined . . . 83
  10—The pieces which regenerated incompletely . . . 88
III—DISCUSSION . . . 91
IV—SUMMARY . . . 93
V—REFERENCES . . . 94

I—INTRODUCTION

1—General

In the previous investigations of this series (1931, 1933) we operated in certain ways on stem apices of *Lupinus albus*, and thereby caused big changes in the positions of the subsequent leaves. We concluded that these changes strongly supported VAN ITERSON's theory of phyllotaxis (1907), and further that each new leaf arises in the first space that attains both a certain minimum width and also a certain minimum distance below the extreme tip or "growing-point." But the changes produced did not include a change from a spiral to a whorled phyllotaxis, and consequently they do not answer the question whether the difference between spiral and whorled phyllotaxis depends on some intrinsic difference in the properties of the stem apices, or whether it can be explained in some other way.

Now according to SCHWENDENER (1878), WEISSE (1889), ROSENPLENTER (1890), VAN ITERSON (1907) and others, if one observes the ways in which spiral and whorled phyllotaxis systems originate in axillary buds and embryos, one can explain them on the theory that the position in which each new leaf arises depends on the positions of the older members with which it makes contact. Thus according to VAN ITERSON (1907) in species with decussate phyllotaxis—that is with alternating pairs of opposite leaves—each of the first two young leaves after the cotyledons covers an arc of less than 180°, so that there is room for them to arise opposite one another and at the same level, in the plane at right angles to that of the cotyledons. But in many species with spiral phyllotaxis, the first two leaves after the cotyledons cover arcs of more than 180°, and consequently they arise opposite one another, but at different levels. Then the arc of each new leaf falls to less than 180°, and consequently leaf 3 arises not directly above leaf 1, but between leaves 1 and 2 on one side of the apex or the other, and nearer to leaf 1 since leaf 1 is lower than leaf 2. The system is then asymmetric, and a spiral phyllotaxis follows. (Further investigation is necessary to determine how it is that after leaf 2 two simultaneous and united leaves do not arise, one on each side of the apex.) Other species again are at first decussate, and then become spiral through a fall in the arcs of the young leaves, in rather a similar way.

The belief that the difference between whorled and spiral phyllotaxis does not depend on any intrinsic difference in the properties of the apices is strongly supported by some valuable experiments and observations of WEISSE (1894), who found that in a large number of species with whorled phyllotaxis, *adventitious* buds usually showed spiral phyllotaxis. These adventitious buds sometimes originated naturally, and sometimes from the surfaces of wounds which he made on the stems by cutting away the bases of the normal axillary buds in various ways. He was able to explain the positions of the first few leaves of the spiral buds in terms of the asymmetric shapes of the spaces from which they arose, and he concluded that the phyllotaxis is not fixed, but depends on the way in which each bud originates.

We regret that previously we did not know of this work of WEISSE. For if we had known of it, we should not have written that the theories of phyllotaxis " have never been tested by direct experiment " (SNOW and SNOW, 1931, p. 4). Nevertheless a still more direct test would be to try, by a suitable operation on the stem apex, to convert a whorled phyllotaxis system into a spiral one, and the results of such an attempt are here reported.

2—*Materials and methods*

Young shoots of *Epilobium hirsutum* were found to have apices that were suitable for the experiments, being just large enough to be operated on, though smaller than the apices of *Lupinus albus* operated on previously. Shoots of ash have much larger apices, but they would be more difficult to bring under the microscope while attached to the tree. The decussate rosettes at the ends of runners of *Epilobium hirsutum*, growing near Oxford, begin to elongate rapidly in April. They are strictly decussate and continue so until the very end of May, or early June. Their apices then gradually pass into the flowering condition, and this transition can easily be recognized from an increasing precocity of the axillary buds. For while the plant is forming only vegetative axillary buds, these, which are formed in the axil of every leaf, first become visible in the axils of the youngest pair of leaves but two, as was observed by the method described in the next section. But at the very end of May the plant begins to form in the leaf axils the buds of inflorescences, and a little later those of flowers; and these arise at about the same time as their subtending leaves, and also differ from the vegetative buds in shape, being more rounded. The inflorescence buds are intermediate in precocity and shape. When the inflorescence or flower buds begin to be formed, the phyllotaxis of the main apex becomes spiral, as in many other species.

For our experiments we dug up short young shoots in April or early May, planted them in boxes, and allowed them about a week to recover. We then exposed the apices, and operated on them under a binocular dissecting microscope as before. After times ranging from 14 to 20 days (or occasionally longer), we pickled the apices, and subsequently embedded them in collodion, cut them free-hand, and drew the sections under a drawing eye-piece or projection apparatus as before. In the sections it could clearly be seen that the apices had not begun to form the buds of inflorescences or flowers during the period of experiment, except in two plants, Nos. 37 and 58, in which they had begun to do so in the axils of the very youngest leaves present. Since, therefore, the induced changes of phyllotaxis began at once with the first leaves that arose after the operations, they were in no way connected with the normal transition to spiral phyllotaxis, which only takes place when buds of inflorescences or flowers begin to be formed. During the experiments it was found desirable to keep on removing any of the older axillary buds that began to grow out.

3—*The normal apex of* Epilobium hirsutum

A large number of normal vegetative apices of *Epilobium hirsutum* were examined, some by sections and others by dissecting out the living shoot apex with the youngest visible pair of leaves and the bases of the next older pair attached to it. When dissected out, the preparation was placed in a thin film of water on a slide and observed as a solid object by transmitted or reflected light at magnifications up to 90. The dissections were found much the more instructive. The youngest visible pair of leaves will be called 1 and 1, and the next older pair 2 and 2, and so on.

When the leaves 1 and 1 are very young—that is, at the beginning of a plastochron—the stem apex between them has the shape, as seen from above, of a rather elongated ellipse, of which the longer diameter is at right angles to a line joining the leaves. The apex grows throughout the plastochron, but more rapidly in the direction of its shorter than of its longer diameter, so that at the end of the plastochron it is less elongated and more nearly square than at the beginning. Thus in three apices in which the leaves 1 and 1 were small, the ratios of shorter to longer diameter were 0·47, 0·5 and 0·5, while in the two apices in which these leaves were large they were 0·68 and 0·69. This point seems worth noting, since WEISSE (1894, p. 284 *seq.*) has stated that the exact opposite is the rule for the numerous decussate species (not however including *Epilobium hirsutum*) which he has examined. A transverse section of an apex with leaves 1 and 1 fairly large is shown in fig. 2, and longitudinal sections through the apex at various stages are shown in fig. 1. Fig. 1, *a*, shows a section through the plane of leaves 2 and 2 and through the regions from which the next pair of leaves was due to arise. This apex was near the end of a plastochron. Fig. 1, *b* and *c*, show sections through the plane of the leaves 1 and 1 in two shoots, in one of which these leaves were very small, while in the other they were rather small. In the latter the stem apex has risen up slightly between the leaves. When the leaves 1 and 1 are large, the apex arises up between them a little more still, though it does not become so pointed as the apex of *Lupinus albus*, as was observed in dissected preparations.

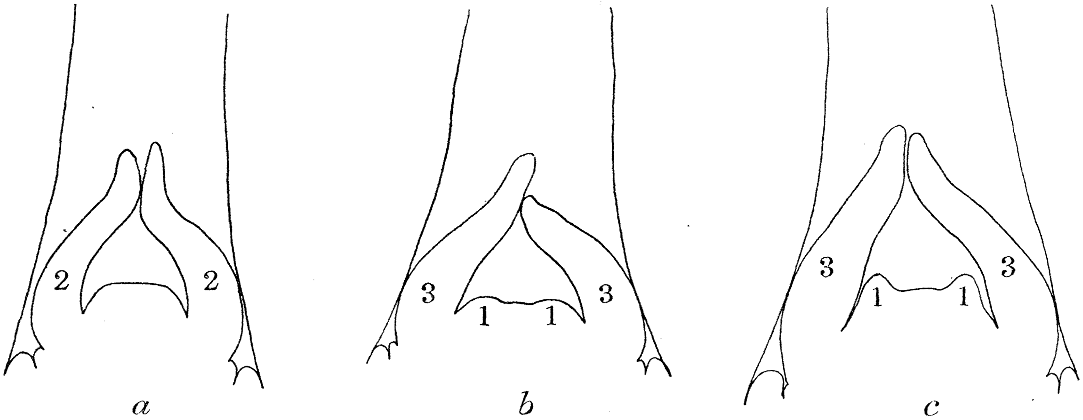

FIG. 1—Longitudinal sections of normal apices of *Epilobium hirsutum*. *a*. Through plane of leaves 2 and 2 towards end of plastochron. *b* and *c*. Through plane of leaves 1 and 1 at beginning and end of plastochron. × 71

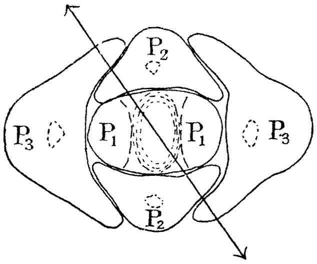

FIG. 2—Transverse section of a normal apex with an arrow showing position of cut in experiments. × 71

The youngest leaves 1 and 1 are not circular in outline at their insertions, but slightly elliptical as seen from a direction perpendicular to the surface of the apex, even when they first become visible. Their transverse diameter is the longer, and during their first plastochron they extend transversely still further, so that they continually subtend larger angles at the centre. The largest angle subtended by a leaf 1 in these apices was 144°, and this may be taken as being roughly the angle subtended at the end of the first plastochron. After their first plastochron the young leaves continue to extend transversely, and finally they meet on each side of the axis.

4—*The nature of the operations and the resulting regeneration*

The operation attempted was to split the apex by a vertical cut in a median diagonal plane, in the manner indicated by the straight line in fig. 2. When the split was successfully made in a median or nearly median plane, new apices were formed by regeneration from both halves, and they continued to grow and form leaves, as in previous experiments by one of us on *Vicia Faba* and *Lupinus albu* (Pilkington, 1929). The extreme tips of the new apices, or the new growing-points, as they will be called, must have been formed at a little distance on each side of the cut, as in the previous experiments (1929), since the regenerated apices were rounded off on all sides.

But often, since the operation was difficult, the cut fell rather far from the median plane, and then only the larger of the two pieces formed grew on indefinitely. The smaller piece then sometimes regenerated a feeble new apex which produced at most two leaves of about normal size, and was then used up or nearly so, and sometimes (if the cut was still further from the median) it did not regenerate at all. Since these smaller pieces were found to be of unexpected interest, in some of the later experiments the cuts were deliberately placed not quite in the median plane. The cuts varied also in the exact angle which they made with the line joining the centres of the two youngest leaves; for this angle was always intended to be 45°, but actually it varied and was usually rather more than 45°. When both halves regenerated, the new apices often grew out in widely diverging directions, especially when the split had been rather shallow. So in order to cut truly transverse sections through both apices, it was then necessary to tilt the razor into a different plane half-way through each cut.

The reason for choosing to split the apex in a diagonal plane was that by this operation the symmetric shoot apex is divided into halves in each of which the contour line formed by the outlines of the wound and the uppermost leaves is asymmetric. Consequently, on the basis of the theory here adopted, a change to an asymmetric—that is, spiral—phyllotaxis was to be expected in the regenerating apices.

The pairs of leaves visible at the time of operation will be called P_1 and P_1, P_2 and P_2, etc., P_1 and P_1 being the youngest: the leaves arising after the operation will be called I_1, I_2, etc., I_1 being the first to arise.

II—Results of Experiments

5—*Preliminary review of results*

The number of plants of which the apices were split was 35, apart from a few plants in which either the operation or the section cutting was found to have been faulty, and one plant which flowered rather soon. In 15 of the 35 plants both halves of the split apex regenerated completely, and formed new apices strong enough to grow on indefinitely, while in the other 20 (in which the split was rather far from the median plane) only the larger of the two pieces did so. Thus the experiments produced $(2 \times 15 + 20) = 50$ completely regenerated apices. Of these 50 apices

37 developed spiral phyllotaxis, 5 were, or became, nearly decussate, and 8 formed a certain other peculiar arrangement in which certain leaves were joined. These apices, therefore, fell into three main groups, which will be described separately. The remaining 20 halves, which were too small to regenerate new apices capable of growing on indefinitely, were nevertheless of interest in other ways. The pieces formed by one split often developed differently, but they will usually be illustrated together. One of the pieces of each pair—the larger if they differ in size—will be called " A," and the other piece " B."

6—*The spiral apices*

The most usual manner in which spiral phyllotaxis was developed is well shown by plant No. 90, fig. 3, in which both halves regenerated and formed very similar spirals. In fig. 3, *c*, a section is shown just above the level of the insertions of the P_1's, the plane of the split being indicated by an arrow. It will be noticed that the P_1's and P_2's are no longer opposite to one another, the explanation being simply that since the operation the half-axes have diverged from one another in the diagonal plane at right angles to the plane of the split.* The inner edges of both P_1's have been just cut by the split, but no marks of the wound can be seen on the half-axes, since in this species the operations leave little or no visible wound scar.

In order to understand how the spirals developed, one must consider the symmetries of the half-apices formed by the operation. If in fig. 3 one looks at either half-axis from the direction of the P_1 belonging to it, one sees that the plane of the split runs away obliquely to the right. Consequently on the right-hand side of each half-apex there must have been more space available for leaf formation between P_1 and the wound than on the left-hand side. It is therefore in accordance with expectation on the theory adopted, that on each half-apex I_1 arose on the right with its centre somewhere between P_1 and the wound, *see* fig. 3, *b*. I_2 then arose on the left of each half-apex, with its centre between P_1 and the wound, since this was clearly where the necessary space must next have become available. I_1 and I_2 were not exactly opposite, but converged considerably towards the wound, and consequently I_3 in each apex arose on the side away from the wound in the larger angle between I_1 and I_2, and rather closer to I_1, since I_1 was at the lower level. Thus I_1, I_2 and I_3 formed a cycle of leaves in spiral sequence, the genetic spirals on both apices winding counter-clockwise. The subsequent leaves continued the spirals, each leaf arising in the first available space so far as could be judged. Another plant which gave a very similar result is shown in fig. 4, No. 124. The divergence angles between the successive leaves of the spiral apices are given in Table I and will be commented on in the next section.

The contacts made by the successive leaves varied a little in different apices; but I_3 regularly made contact with I_1 and I_2, and sometimes with P_1 also ; I_4 and I_5

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* Actually in No. 90 the two apices were sectioned separately, so that their relative positions had to be estimated. But in other plants in which the apices were sectioned together they were found to occupy similar positions with the P_1's no longer opposite, for instance in No. 16, fig. 11.

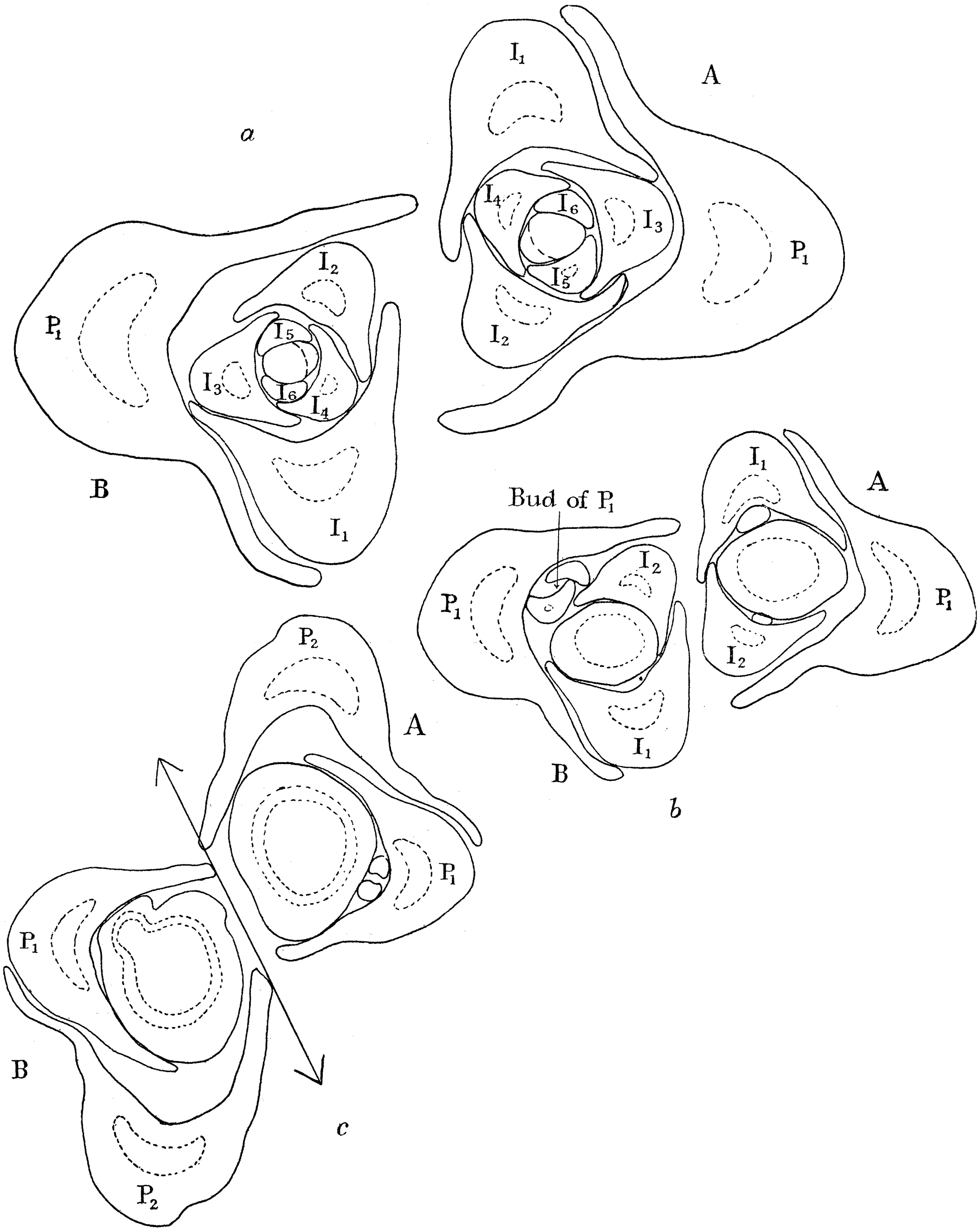

FIG. 3—No. 90, A and B. Both apices are spiral. Sections *a*, *b* and *c* at different levels from above downwards. The arrow marks roughly the plane of the cut. *a* × 56, *b* × 38, *c* × 31

usually made contacts 1, 2 and 3 (that is—they made contact with the first, second, and third older leaves) ; I_6 and later leaves usually made contacts 2 and 3, as in Nos. 90 and 124A, though in a few apices they made contacts 1, 2 and 3. Thus there was usually a gradual change from a system of contacts 1 and 2, to one of contacts 2 and 3, and this was due to the fact that the older leaves covered larger arcs than the younger ones. Probably this was partly because the regenerating apex was at first small, and then gradually regained a normal size : but some allowance must be made for the fact that the older leaves had extended laterally since they were first formed.

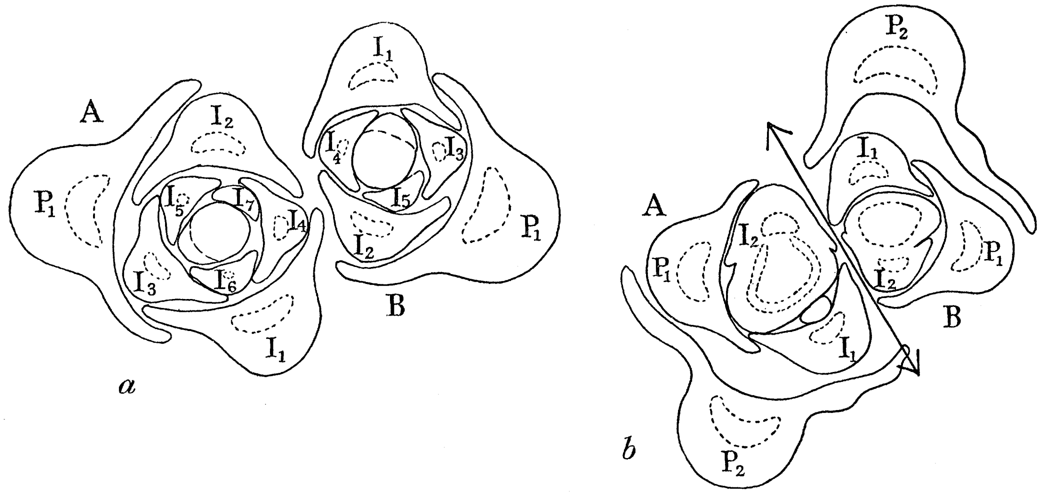

FIG. 4—No. 124, A and B. Both apices are spiral. Sections *a* and *b* at different levels. *a* × 56, *b* × 38

TABLE I—THE SPIRAL APICES AND THEIR DIVERGENCE ANGLES IN DEGREES

Number of apex	Difference of level between I_1 and I_2	$\angle I_1–I_2$	2–3	3–4	4–5	5–6	6–7	7–8	8–9	9–10
GROUP 1—TEN APICES IN WHICH THE ANGLES WERE FAIRLY CONSTANT THROUGHOUT										
10	big	136	141	141	131	—	—	—	—	—
*16B†	medium	144	142	135	140	136	143	—	—	—
20	big	156	141	141	129	138	142	—	—	—
47A	big	144	126	143	141	144	139	—	—	—
*49	big	144	133	141	146	133	144	—	—	—
90A	big ?	139	132	134	144	143	—	—	—	—
90B	big ?	135	139	130	134	—	—	—	—	—
94A	big	138	144	130	133	140	—	—	—	—
107B	medium	138	140	131	145	—	—	—	—	—
124A	big	142	133	145	139	140	132	—	—	—

* Those apices in which I_1 and I_2 diverged from the wound.

† The letters A and B in column 1 denote the two new apices of each plant : when only one apex was regenerated completely, the letter A is omitted : when two apices were regenerated completely, but only one was spiral, the other apex will be found in Table II, p. 79, or III, p. 83. Question-marks mean approximate values.

TABLE I—(continued)

Number of apex	Difference of level between I_1 and I_2	$\angle I_1$–I_2	2–3	3–4	4–5	5–6	6–7	7–8	8–9	9–10
GROUP 2—SEVEN APICES IN WHICH THE ANGLES BECAME FAIRLY CONSTANT AFTER OSCILLATING AT FIRST										
53A	big	173	115	140	141	146	134	—	—	—
73	big	168	122	137	135	137	—	—	—	—
86	fairly big	164	122	145	138	144	—	—	—	—
89	medium	153	119	141	142	142	—	—	—	—
*123A	small	159	122	150	142	135	—	—	—	—
124B	—	165	110	152	132	135	—	—	—	—
125A	big	171	115	151	144	145	—	—	—	—
GROUP 3—THIRTEEN APICES IN WHICH THE ANGLES OSCILLATED REGULARLY										
4	?	170	117	148	120	160	—	—	—	—
33A	big ?	179	121	143	137	151	—	—	—	—
36	small	154	103	168	122	151	—	—	—	—
37A	very small	—	—	160	118	151	127	157	108	—
*39	fairly big	172	112	142	125	162	110	160	124	157
45	big	154	117	145	140	150	134	146	—	—
*53B	small	185	94	159	112	173	108	—	—	—
*55	medium	141	121	161	126	146	136	146	136	148
*57	—	178	92	175	110	156	117	—	—	—
58	medium	155	118	153	129	147	139	—	—	—
81	big	151	124	144	133	154	136	148	—	—
88	small	150	115	166	112	166	108	162	—	—
*131	big	168	113	148	128	147	126	—	—	—
GROUP 4—THREE APICES IN WHICH THE ANGLES OSCILLATED REGULARLY, EXCEPT THAT THE SECOND AND THIRD ANGLES WERE BOTH SMALL										
2A	big	148	127	131	156	123	—	—	—	—
2B	big	159	130	125	151	120	—	—	—	—
*95†	big ?	161 ?	123 ?	131 ?	153	136	144	136	152	126
GROUP 5—FOUR APICES IN WHICH THE ANGLES WERE IRREGULAR										
47B	big	170	126	137	136	155	124	—	—	—
*78	—	178	107	162	137	134	126	171	96	176
*110A	big	187	119	129	143 ?	—	—	—	—	—
*125B	big	159	160	108	145	—	—	—	—	—

* Those apices in which I_1 and I_2 diverged from the wound.

† In No. 95, the following further angles were measured : 10–11, 158° ; 11–12, 123° ; 12–13, 153°

Positions approximately similar to those of I_1 and I_2 in the apices described already were occupied by these leaves in all the regenerated apices except one, No. 37A, which will be described specially. (Naturally in some plants the plane of the split ran away obliquely to the left instead of the right, and then I_1 arose on the left and I_2 on the right.) But the exact positions of I_1 and I_2 varied considerably, and so, in consequence, did the angle between them. For in 25 of the 37 spiral apices I_1 and I_2 converged towards the wound, as in the apices already described, the angles between their centres ranging from 135° to 179°. In these apices therefore the larger angle between the centres of I_1 and I_2 was on the other side of the apex above P_1, and so also, as was noted, was the larger gap or depression between or above the edges of these leaves. Consequently I_3 arose on the side above P_1, as was to be expected from the theory here adopted.

But in ten other spiral apices, which are marked by asterisks in Table I, I_1 and I_2 converged towards P_1, the angles between them on that side ranging from 141° to 178°; and I_3 arose on the side above the wound. An example is No. 131A, fig. 5. This was again according to expectation, since in these apices not only the larger angle between the centres of I_1 and I_2, but also the larger gap or depression between or above their edges was on the side above the wound, as was noted for all these apices except one, No. 95A, of which the sections showing this gap were missing.

There remain two apices, Nos. 110A, fig. 6, and 53B, also marked by asterisks in Table I, in which the larger angle between the morphological centres of I_1 and I_2 was on the side above the wound, and yet I_3 arose on the side above P_1. But in these apices the angles between the centres of I_1 and I_2 were close to 180°, being 173° and 175°, and the I_2's were asymmetric and extended further on the side above the wound than on the side above P_1, so that in No. 110A the larger gap between the edges of I_1 and I_2 was clearly on the side above P_1, *see* fig. 6, *b*. In No. 53B the edges of I_1 and I_2 just met on both sides of the apex, so that the spaces available on each side for the next leaf seem to have been practically equal. In this apex I_3 and I_4 did indeed arise at practically the same level, though I_3 was for some reason very slightly the larger.

Results similar to No. 110A, in which a leaf arose in the larger gap between the edges of two previous leaves although this gap was in the smaller angle between their morphological centres, were reported in both the previous papers on *Lupinus albus* (1931, p. 9, and 1933, p. 383). They indicate that the positions in which new leaves arise depend upon the positions of the *outlines* of the previous leaves, and not of their centres, *see* 1933, p. 396.

The positions, therefore, of I_3 and subsequent leaves in the spiral apices can be readily explained; but it is more difficult to account for the variations in the exact positions of I_1 and I_2, since these may have been due to several varying factors, of which one at least could not be measured. In most of the apices, as has been pointed out, I_1 and I_2 were not opposite but converged towards the wound, and probably this was largely because the extreme tip or growing-point of the regenerating apex had shifted away from the wound, and so also had the young stele beneath it, *see* section 4. But it was not found possible to measure the shift of the growing-point, and it is probable that variations in the amount of this shift were partly responsible for the variations in the angle between I_1 and I_2.

There remains, however, the question how it was that in several apices I_1 and I_2 diverged from the wound. In the hope of answering this question some of the other varying factors were measured approximately, and were tabulated both for the spiral apices and also for the other regenerated apices, not yet described, which are equally relevant to the present question. These factors are, firstly, the stage of the

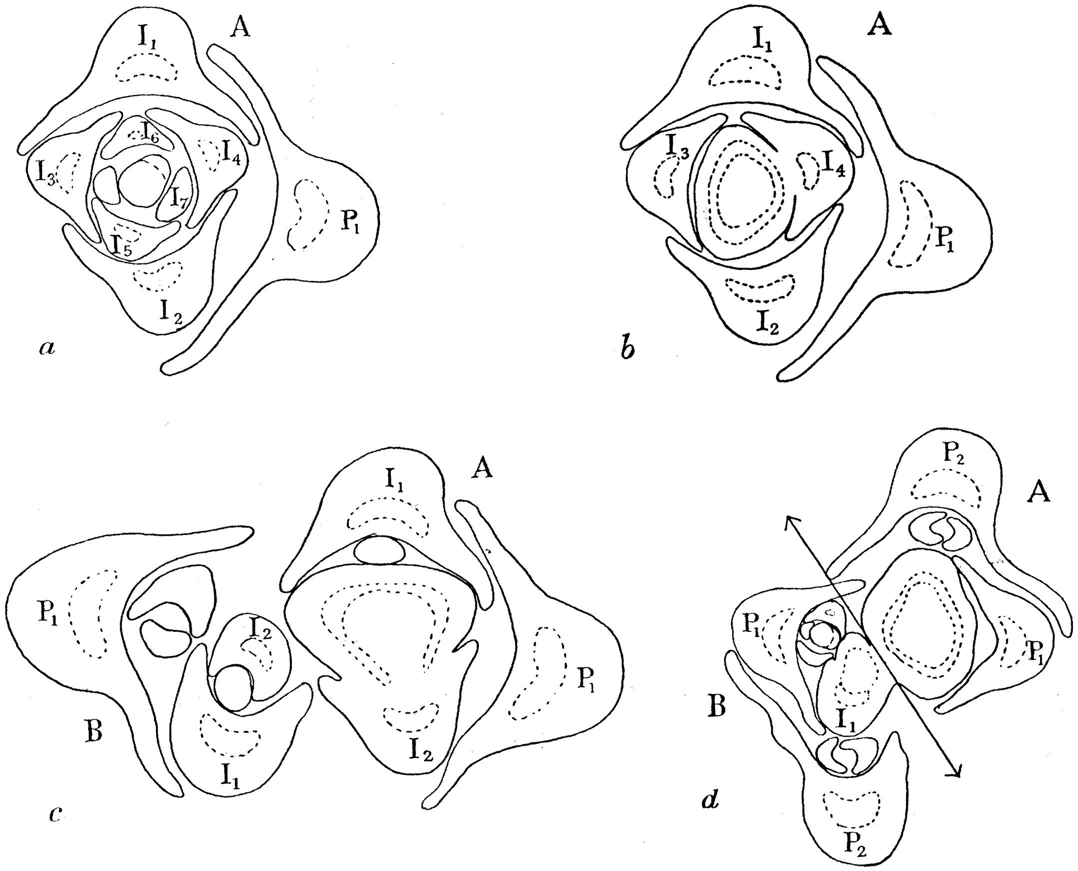

FIG. 5—No. 131, A and B. A is spiral. *a* and *b* show sections of A ; *c* and *d* of A and B at different levels. *a*, *b* and *c* × 56, *d* × 31

plastochron at the time of operation, as indicated by the size of P_1 at that time ; secondly, deviations of the splits from the exact median plane ; thirdly, variations in the obliquity of the split on either side of the exact diagonal plane, *see* section 5 ; fourthly, the depth of the split. It was found that the only one of these factors which was clearly correlated with the variations in the angle I_1–I_2 was the depth of the split, and this factor was correlated in the sense that in those plants in which both halves regenerated completely—the " doubles " as they may conveniently be called—it was very often the shallowest splits which caused I_1 and I_2 to diverge from the wound, on one-half at least. Thus out of 9 apices belonging to " doubles," in which I_1 and I_2 diverged from the wound, seven were formed on plants in which, as for instance in No. 110, fig. 6, the halves were found to be united above the level of the upper contour of the insertion of P_1 (Nos. 125B, 53B, 16B, 113B, 110B, 110A, 123A), while for one, No. 33B, the level could not be determined since the necessary sections were missing. (The remaining apex of these nine was No. 37B.) On the other hand, out of 21 apices belonging to " doubles " in which I_1 and I_2 converged *towards* the wound, only five were formed on plants in which the halves were united

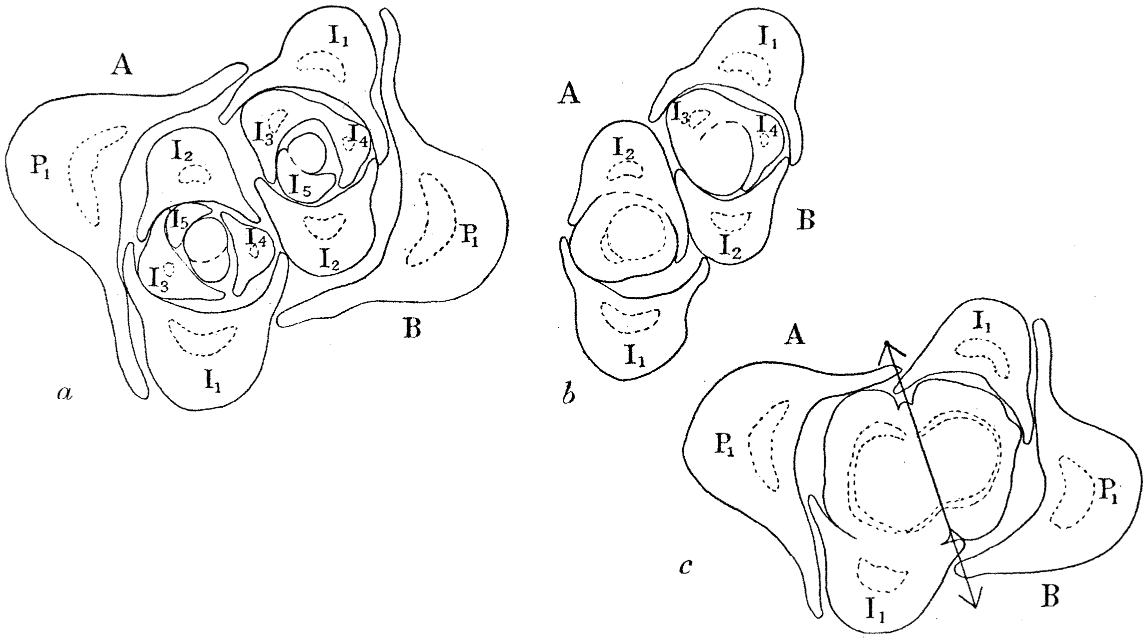

FIG. 6—No. 110, A and B. A is spiral, B has I_3 and I_4 united. Sections *a*, *b* and *c* at different levels, all × 42

above the level of insertion of P_1 (Nos. 125A, 53A, 16A, 113A, 123B), while for one, No. 33A, the level could not be determined.

The following explanation of these facts may be suggested. The surface of the normal apex in this species rises only slightly above the bases of the youngest leaves, especially in the first half of the plastochron, as was pointed out in section 3. Consequently when the apex was first split the base of the wound must always have been well below the upper contour of the insertions of the P_1's, and even the top of the wound cannot have been more than a very little above that level. It is therefore clear that in the plants in which the halves were afterwards found to be united above the level of insertion of the P_1's, the greater parts of the cut surfaces and probably the whole of them must have re-united. These re-unions would not by themselves affect the positions of I_1 and I_2, since in any case leaves are not formed from the surfaces of deep wounds such as these, as we found previously (1931, 1933). But if it may be supposed further that in these plants the inner sides of the regenerating apices united also for a short distance *above* the wound, then it will follow that their union must have made some small region directly above the wound on each regenerating apex unavailable for leaf formation. Consequently it can then be understood that in these plants I_1 and I_2 arose with their centres further away from the wound—far enough to allow room for the sides of these leaves to be formed between the leaf-centres and the united region. For we have shown previously (1933) that the centres of leaves are not formed in positions that would allow no room for their sides.

This suggested explanation is specially probable for the apices belonging to plants 110, fig. 6, and 113, in which the halves were united even above the insertions of the I_1's. But it cannot easily be applied to the "singles"— that is, the plants in which only one apex regenerated completely—since in the "singles" re-unions above the level of the P_1's were much less common. Thus out of nine "singles" in which I_1 and I_2 diverged from the wound, only two had their halves united above the level of the P_1's: these two were No. 131A, fig. 5, which was very nearly a double, and No. 95A. It therefore seems that in the singles at least there must have been some undetected varying factor which affected the positions of I_1 and I_2.

Two of the 37 spiral apices differed considerably from the others, and must be described specially. One of these was No. 37A, fig. 7, which was mentioned previously as being the only apex in which I_1 and I_2 arose in altogether unusual positions. Of these two leaves, the leaf labelled I_1 in fig. 7 was slightly the larger, though it was inserted at practically the same level as the leaf labelled I_2. But if it had been permissible to interchange the labels of these two leaves, the whole apex would have appeared quite similar in its phyllotaxis to the other spiral apices. Actually, however, when I_1 and I_2 are labelled in the manner shown in fig. 7, it can be seen that they are situated on the opposite sides of the apex from the usual; for the cut, as seen from P_1, runs away obliquely to the right and yet I_1 arises on the left; moreover, I_3 and I_4 both arise closer to I_2 than to I_1. Thus the peculiarity of this apex is essentially that the leaf which must be labelled as I_2 is situated at just the angular position at which I_1 was to be expected, and also acts, in determining the positions of the subsequent leaves, just as if it were I_1. We cannot explain this peculiarity, but suspect that it may have been somehow due to some slight secondary injury inflicted accidentally at the time of operation. For in a few other operations secondary injuries were certainly inflicted, as was revealed by wound-scars afterwards, so that the resulting apices had to be rejected. But unfortunately in this species the amount of wound scar formed is usually very slight, so that a slight secondary injury may easily leave no visible trace.

The other peculiar apex was No. 78A, fig. 8. In this apex I_1 and I_2 arose in about the usual positions, diverging very slightly away from the wound, but I_2 was united with I_3, and so also was I_5 with I_6, and I_8 with I_9. In spite of the united leaves the arrangement is spiral; for I_2 was inserted slightly lower than I_3, I_5 was lower than I_6, and I_8 lower than I_9, as was clear from sections through the insertions of these leaves. (One such section, through the insertions of I_5 and I_6, is shown in fig. 8, *b*.) Also the arrangement, though peculiar, has a regularity of its own, as can readily be seen from the figure. But with the very youngest visible leaf, I_1, the regularity ceases ; for this leaf is not arising in the position necessary for continuing the system. No other system was found at all like this.

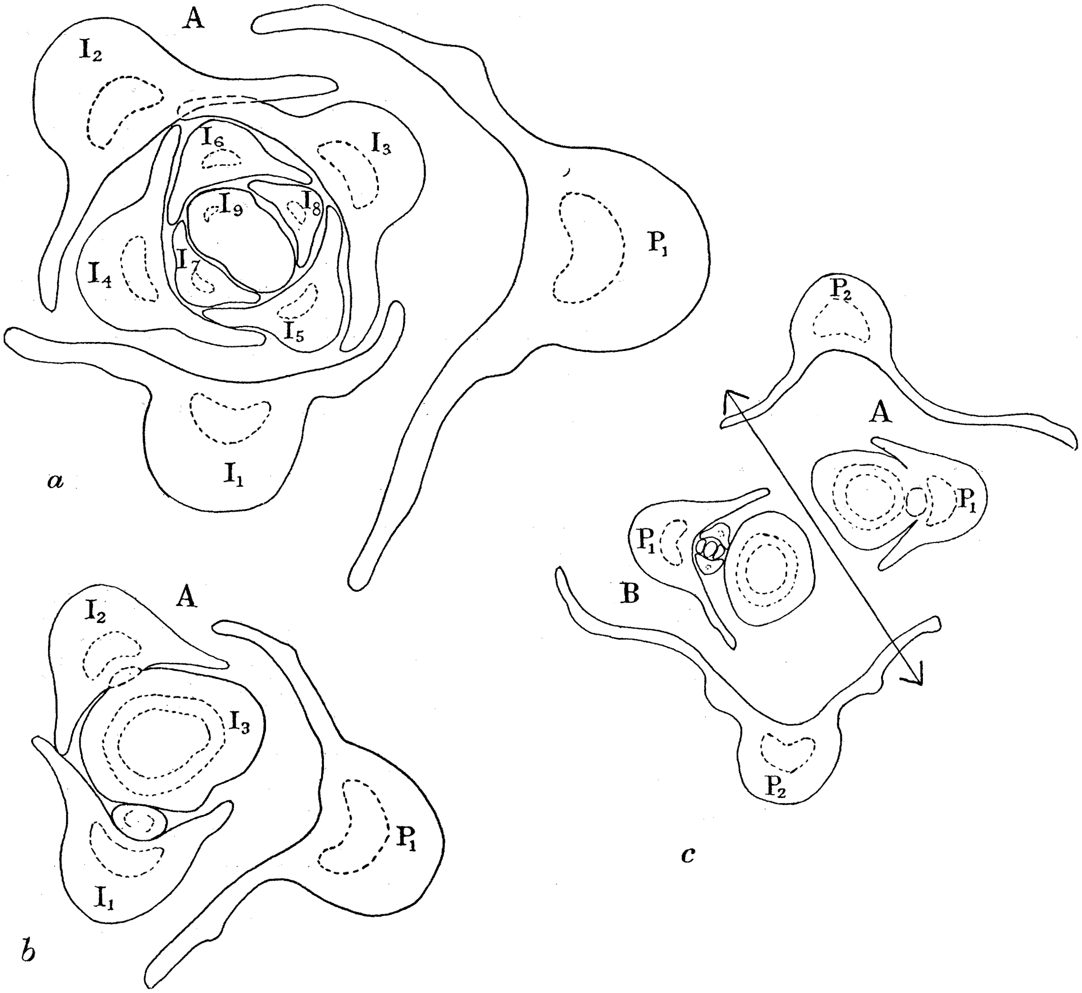

FIG. 7—No. 37A. A peculiar spiral. *a* and *b* show sections of A ; *c* of A and B, at different levels. *a* × 56, *b* × 38, *c* × 29 approx.

7—*The divergence angles in the spiral apices*

The divergence angles between the morphological centres of the successive leaves in the spiral apices, from the angle I_1–I_2 up to the last angle which could be measured accurately, are recorded in Table I. The apices are arranged in groups according to the peculiarities of the different series of angles. In a first group of ten apices the angles were throughout fairly constant about an approximate mean value of 140° : in these apices the first angle of the series, the angle I_1–I_2, was itself very close to 140°, except in one, No. 20, in which it was 156°. Examples of this group are Nos. 90A and B, fig. 3, No. 124A, fig. 4, and No. 16B, fig. 11.

In a second group of seven apices, the first angle, I_1–I_2, was much above 140°, ranging from 153° to 173°. The second angle was much below 140°, ranging from 110° to 122°, but the third or fourth angle returned nearly to the approximate mean value of 140°, and subsequent angles appeared to remain constant about this value, though unfortunately in this group the fifth or sixth angles were the last that could be measured. An example is No. 123A, fig. 13.

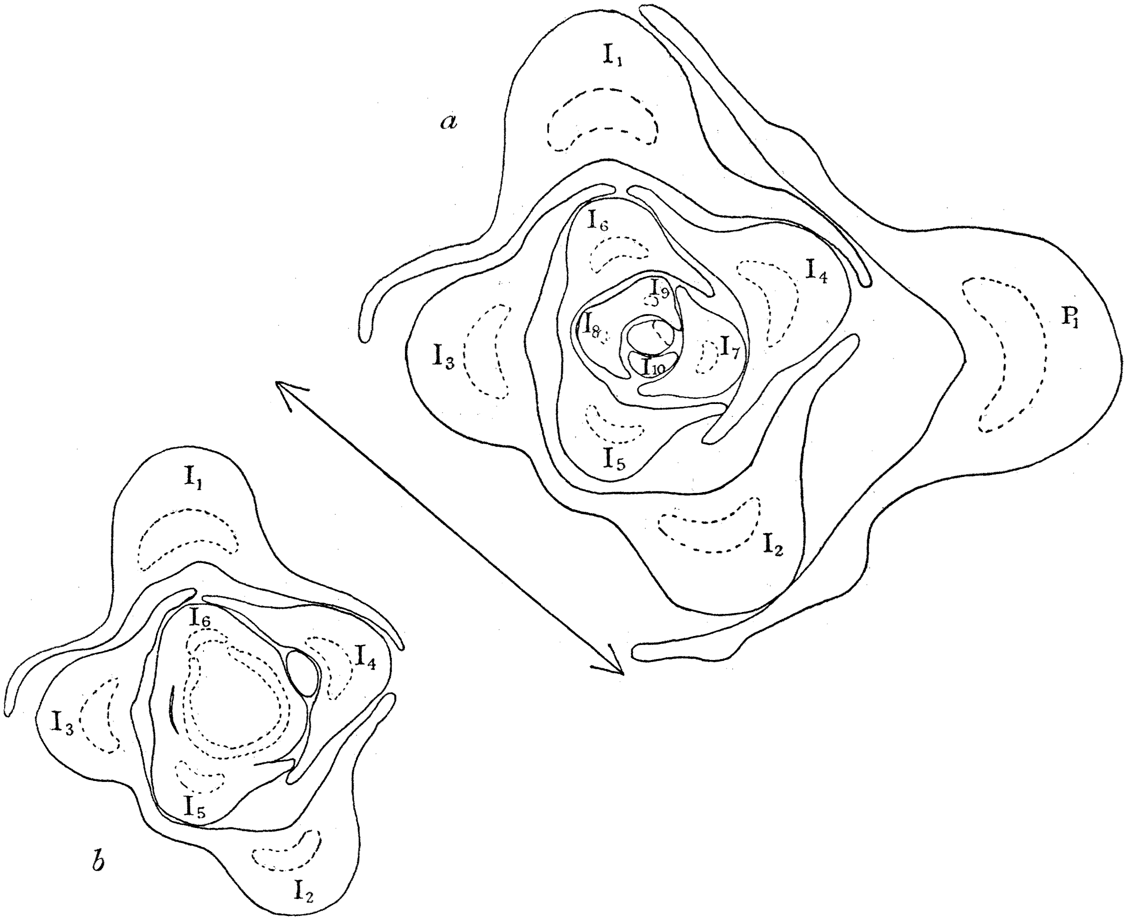

FIG. 8—No. 78A. A peculiar spiral with united leaves. *a* is a composite drawing from sections at different levels. *b* shows the sequence of I_5 and I_6. Both × 38

In a third group of 13 apices the first angle was large, and about the same as in the previous group, ranging from 150° to 185°,* except in one apex, No. 55, in which it

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* The angle I_1–I_2 is always recorded in the table as measured in the direction of the subsequent genetic spiral, even in those two apices, Nos. 110A and 53B, in which, when so measured, it is greater than 180° for the reason explained in the last section.

was 141°. The second angle was small, and the subsequent angles continued to oscillate regularly above and below 140°, even when as many as nine angles were measured. Examples are Nos. 131A, fig. 5, and (from I_3 onwards) 37A, fig. 7.

In a fourth group of three apices the angles oscillated like those of the third group, except that the second and third angles of the series were both small. The fourth angle was large, and subsequent angles oscillated regularly. A fifth group contains four apices in which the angles were irregular: one of these four is No. 78A, the peculiar apex with united leaves described already.

It may be noted that in the apices with oscillating angles the differences between the levels of insertion of successive leaves also oscillated regularly. For the leaves that were separated by large divergence angles were regularly inserted at levels which differed slightly, while those that were separated by small angles were inserted at levels which differed greatly. Thus the phyllotaxis of these apices may be considered as in a sense intermediate between that of the spiral apices with constant divergence angles, and that of the normal "decussate" system with its alternating pairs of opposite leaves. For in the spirals with oscillating angles, any two successive leaves that are separated by a large divergence angle and small difference of level may be considered as being nearly a pair of opposite leaves, and the next pair of nearly opposite leaves lies in a plane nearly at right angles to that of the previous pair, *see* fig. 7, No. 37A. From this point of view the spirals with constant angles are the furthest removed from the decussate system and consequently the most completely asymmetric.

It is not at all obvious how the difference between the apices of groups 2 and 3 of Table I is to be explained. For in both groups the angles I_1–I_2 were much above 140° and were about equally large, and the next angles were much below 140°; and yet in the second group the series of angles became fairly constant at the third or fourth angle, whereas in the third group the angles continued to oscillate. We can only suggest as an explanation that the difference between the levels at which I_1 and I_2 were inserted may have been greater in the second group than in the third. For a big difference between the levels of these leaves would cause I_3 and I_4 to converge more strongly towards I_1, and so would tend to increase the angle I_2–I_3, diminish the angle I_3–I_4, and increase the angle I_4–I_5 again: thus it would tend to obliterate the oscillations. We could not indeed determine by observation that this difference in level was significantly greater in the second group than in the third, though on the average it seemed to be a little greater, *see* Table I; but from transverse sections the differences in level cannot be compared at all exactly.

It was, however, observed that in the first group of apices, in which the angles were constant and fairly close to 140° from the start, the differences between the levels of I_1 and I_2 were on the average distinctly greater than in the third group, in which the angles oscillated continually. This can be understood, since the two factors which together made the system asymmetric were a difference between the levels of I_1 and I_2 and an angle I_1–I_2 differing from 180°. When, therefore, the difference between the levels of these leaves was large enough, and the angle I_1–I_2 was not much above 140°, the subsequent phyllotaxis was of the most completely asymmetric kind—that is, a spiral with fairly constant angles.

8—*The nearly decussate apices*

In five regenerated apices the phyllotaxis was, or became, nearly decussate : some details concerning these apices are given in Table II. In the first four apices the phyllotaxis was nearly decussate from the start, or became so after I_2 ; in the fifth it did not become decussate until later. It would be expected that the apices in which the phyllotaxis became most nearly decussate would be those in which I_1 and I_2 were most nearly opposite and most nearly at the same level. Actually in the first of these apices, No. 33B, the angle I_1–I_2 was 173°, and the difference between the levels of these leaves was small ; in this apex the phyllotaxis was throughout very nearly decussate.

TABLE II—THE APICES THAT WERE NEARLY DECUSSATE, OR BECAME SO

No. of apex	Difference between levels of I_1 and I_2	$\angle I_1$–I_2
*33B	small	173
*37B	small	165
71A	very small	162
94B	medium	162
16A	big	132

* Asterisks and letters A and B have same meaning as in Table I.

In No. 71A the difference between the levels of I_1 and I_2 was extremely small, but these leaves converged distinctly towards the wound, the angle between them being 162°. Consequently the phyllotaxis differed slightly from a regular decussation, and was of a bilaterally symmetric and oscillating kind such as we have often found after these and other operations on this species, having a plane of symmetry bisecting the angle I_1–I_2. A clearer and more extreme example of this phyllotaxis is No. 12, fig. 12, to be described in the next section, though in that apex the system started differently, and the plane of symmetry passed *through* I_1 and I_2. From fig. 12, *a*, it can be seen that a phyllotaxis of this kind passes continually through two alternating phases. In one phase two leaves are formed which are simultaneous but not quite opposite, and these are followed in the next phase by two leaves in the plane at right angles which are opposite but not simultaneous. Then there follow again two leaves which are simultaneous but not opposite, and these converge towards the lower of the two previous leaves, and in the opposite direction from that in which the first pair of leaves converged. A system of this kind will be called an "oscillating decussation."

In No. 37B, fig. 9, the difference between the levels of I_1 and I_2 was again small, but quite distinct, and the angle I_1–I_2 was 165°. The phyllotaxis was throughout very distinctly different from a regular decussation, and may be considered about equally well as being approximately decussate, or as being a spiral with widely oscillating angles, similar to those described in the last section. If it is considered as approximately decussate, the leaves being numbered as in fig. 9, then it must be noted that the system oscillates in the way just described ; for the first two leaves diverge away from the wound, the I_4's converge towards the wound, and the I_6's diverge from it again. But the leaves could also be numbered consecutively along a clockwise spiral.

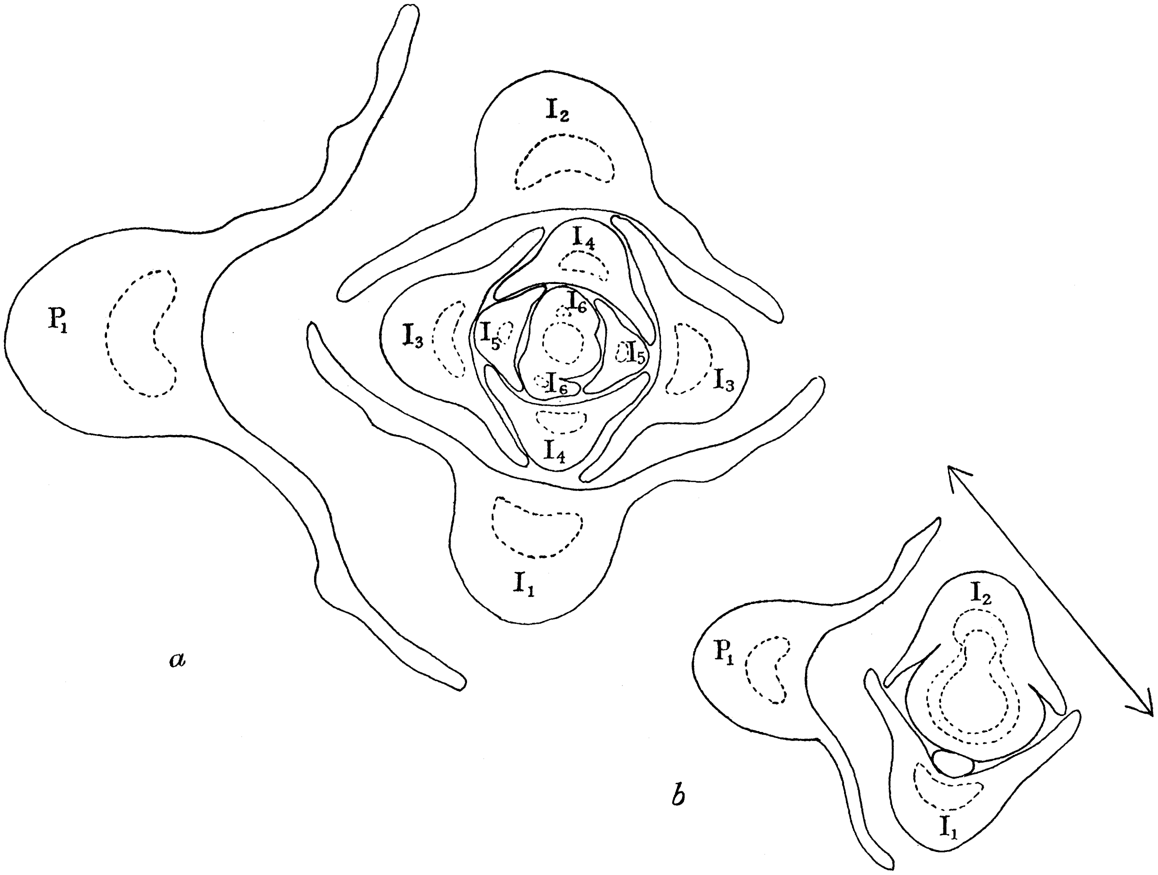

Fig. 9—No. 37B. A nearly decussate apex. Sections *a* and *b* at different levels. For lower level, see fig. 7, *c*. *a* × 56, *b* × 31

In No. 94B, fig. 10, the return towards decussation is at first surprising, since the angle I_1–I_2 was 162° and the difference in level was fairly big. But the explanation is probably that I_1 and I_2 differed very greatly in size, I_1 covering the very large arc of 242° and I_2 covering only 168°. For if these leaves had covered equal arcs, then the next two leaves would have converged greatly towards I_1, since I_1 was inserted much lower than I_2. But actually, since I_1 covered an exceptionally large arc, it can be understood that the next two leaves (the I_3's) arose further from the centre of I_1, and were nearly opposite. Similar returns towards decussation were found in No. 16A, to be described next, and also several times after operations of a different kind on the same species, which are not here reported and which at first resulted in "oscillating decussations." They all took place after the formation of two nearly opposite leaves at different levels, of which the lower leaf covered a much larger arc than the higher leaf. The cause of the difference between the arcs of these leaves was sometimes uncertain and seems to have varied. For in some experiments, as in Nos. 94B and 16A, the difference was mainly due to the abnormally large arc of the lower leaf, while in a few others of the experiments not here reported it was mainly due to the small arc of the higher leaf. In some of these latter experiments it seemed that the higher leaf had been prevented from extending laterally by the axillary buds of the next lower pair of leaves, which converged towards it.

The remaining apex, No. 16A, fig. 11, was peculiar. For the first four leaves,

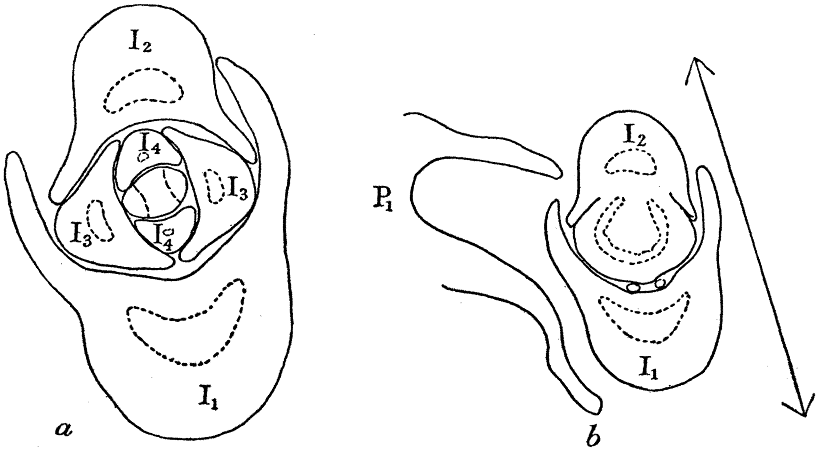

FIG. 10—No. 94B. Sections *a* and *b* at different levels. *a* × 56, *b* × 35

from I_1 onwards, were situated at approximately the same divergence angles from one another as four leaves of a regular counter-clockwise spiral; but yet I_2 was only slightly larger than I_3 and was inserted at the same level as I_3 and united with it, *see* fig. 11, *b*. On the other hand, the difference in level between I_1 and I_2 was very great. Since I_2 and I_3 were at the same level and almost equal in size, and since I_4 made contact with these leaves, the system was thenceforward nearly bilaterally symmetric. I_4 and I_5 arose practically opposite one another, I_4 being at slightly the lower level (as was shown by other sections not illustrated) but covering a considerably larger arc. The system then became nearly decussate, though slight oscillations continued, *see* fig. 11, *c*.

The final return towards decussation, therefore, took place in the same manner as in No. 94B. But the peculiarity of No. 16A is the position of I_2, which appears somehow to have been delayed so that it arose at the same time as I_3. A possible explanation can be suggested, which has the advantage of explaining at the same time a peculiarity in the other apex of the same plant, No. 16B. For it can be seen

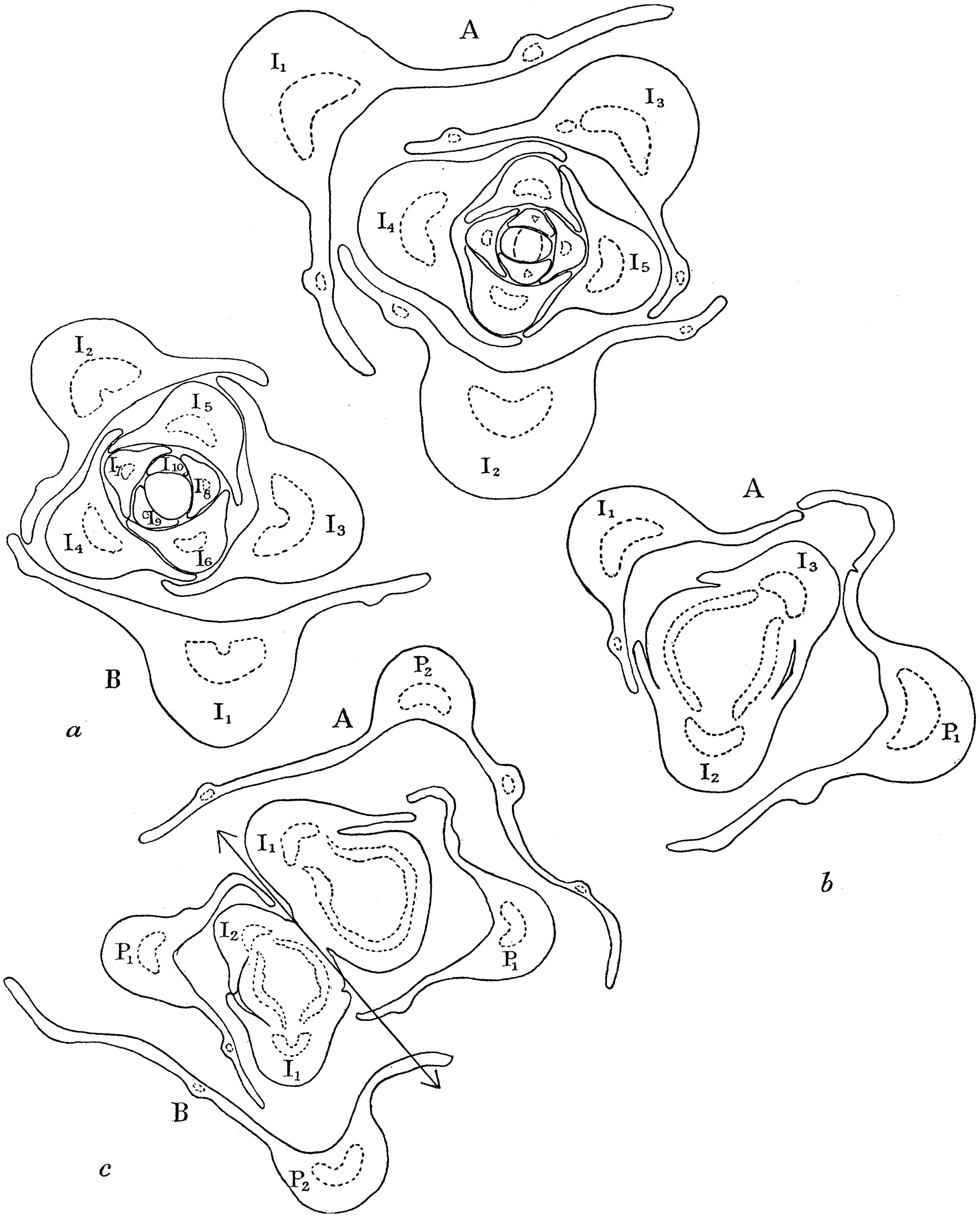

FIG. 11—No. 16, A and B. A returns nearly to decussation, B is spiral. *a* and *c* show sections of A and B, *b* of A alone at an intermediate level. *a* × 35, *b* × 26 approx., *c* × 17

from fig. 11, *c*, that the apices have re-united up to a level above the insertion of the I_2 of the " B " apex, but that the edge of the I_1 of the " B " apex does not reach to the united zone, as it does in other apices. The question therefore arises how it was that on the " B " apex the region between the edge of I_1 and the united zones was not occupied. A quite probable explanation is that at the time when the I_1's were determined, the apices were united in this region also, but that they subsequently broke apart; indeed the shapes of the axes in fig. 11, *c*, suggest that this may have happened. If, however, they did not break apart until some little while after the I_1's were determined, then their temporary union in this region may have caused the peculiar delay in the formation of the I_2 of the " A " apex.

9—*The apices with I_3 and I_4 joined*

In eight apices I_3 and I_4 were joined, and were nearly, or quite, at the same level: examples are shown in figs. 12, 13, 14, 15 and 6, and details are given in Table III. After these leaves the phyllotaxis varied, but I_5 arose approximately opposite the middle of the gap between I_3 and I_4, on the opposite side of the apex, except in No. 113A in which it arose a little to one side and a spiral then started. The subsequent phyllotaxis remained bilaterally symmetric in Nos. 12A, fig. 12, and 71B, while in No. 15A it returned towards decussation in a manner which can be understood from fig. 14, *a*. In the remaining apices no more leaves had been formed after I_5, or not more than one.

TABLE III—THE APICES WITH I_3 AND I_4 UNITED

No. of apex	Difference between levels of I_1 and I_2	$\angle I_1$–I_2	I_2–I_3	I_3–I_4
*12	big	175	119	136
113A	big	175 ?	121	132
*113B	medium	151	148	123
*110B	big	156	149	111
123B	big	167	125	93
15	big	150	145	88
71B	big	149	156	76
107A	medium	160	150	54

* Asterisks and letters A and B have the same meaning as in Table I.

It can readily be understood that the phyllotaxis was usually nearly symmetric after I_3 and I_4, since these two leaves were nearly equal and nearly (or quite) at the same level, and I_5 made contact with them. Consequently the chief question concerning these apices is how it was that I_3 and I_4 arose in this manner, and this question must now be considered. First, it may be noted that in most of these apices there was a big difference in level between I_1 and I_2, *see* Table III, and this must have tended to make I_3 and I_4 converge strongly towards I_1, and so have made them more likely to arise as a united pair, especially when the angle I_1–I_2

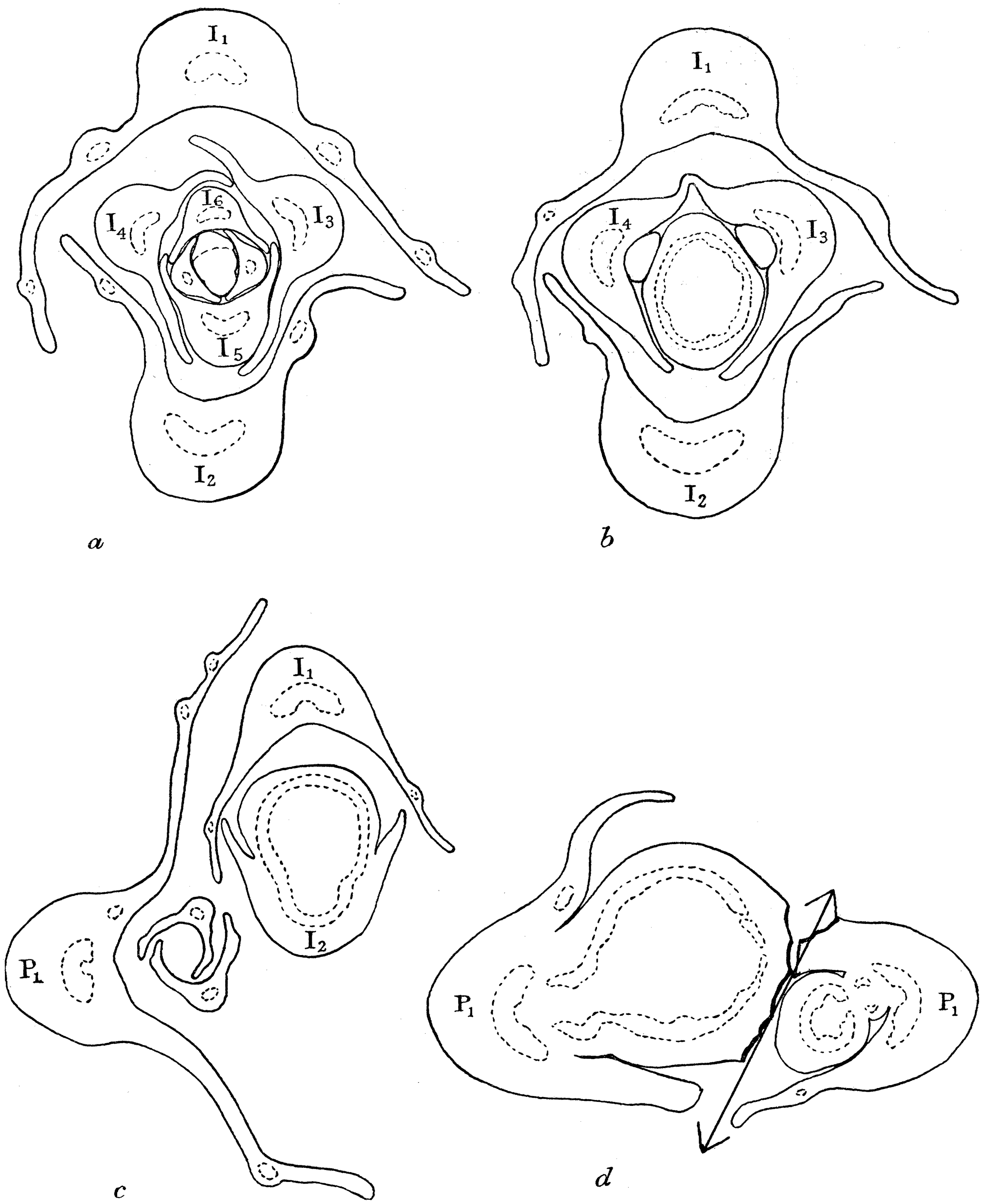

FIG. 12—No. 12, A and B. A has I_3 and I_4 loosely joined. Sections *a*, *b*, *c* and *d* at different levels. *a* and *b* × 34, *c* and *d* × 22

was close to 180°. In the first two apices recorded in Table III, Nos. 12A, fig. 12, and 113A, this big difference in level, together with an angle I_1–I_2 very close to 180°, is the only factor which we can suggest as accounting for the union of I_3 and I_4. In these two apices I_3 and I_4 were only just united, and only near their bases, the angles between their centres being 136° and 132°.

In the next two apices also, Nos. 113B and 110B, fig. 6, I_3 and I_4 were only loosely united, the angles between their centres being 123° and 111°. In these two apices

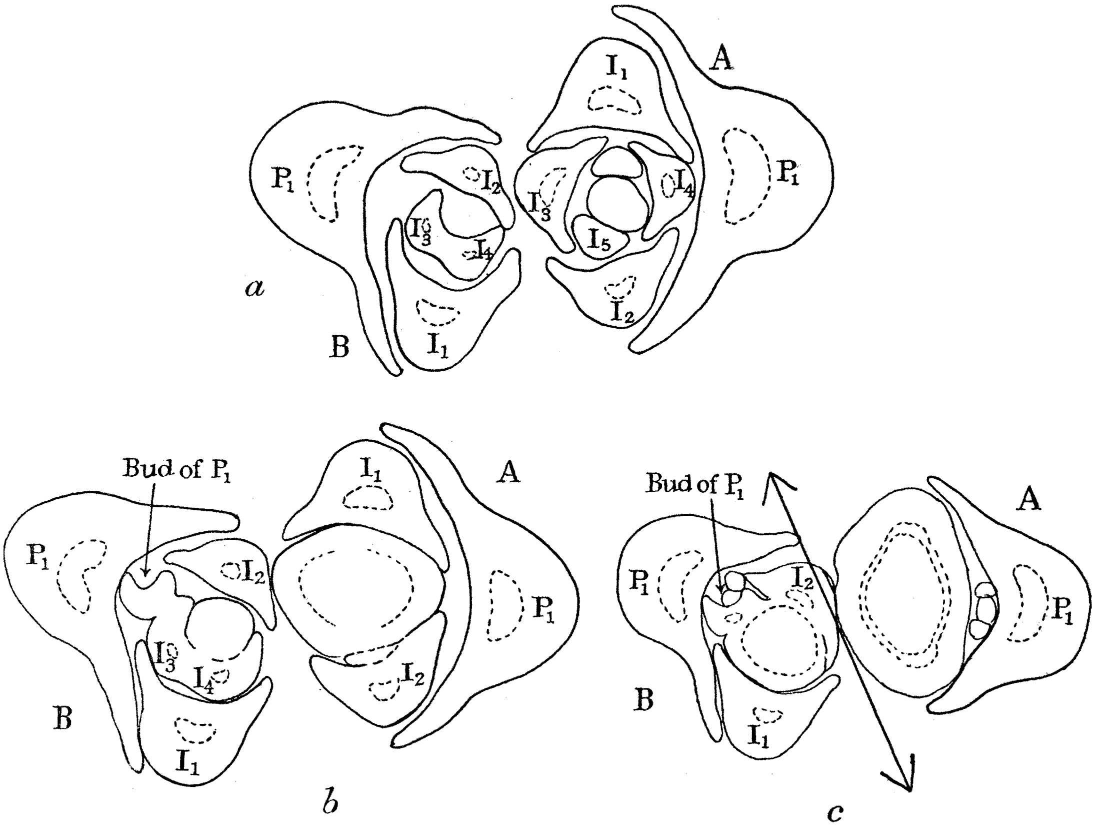

Fig. 13—No. 123, A and B. A is spiral, B has I_3 closely joined to I_4, and joined also to the axillary bud of P_1. Sections *a*, *b* and *c* at different levels, × 56

I_1 and I_2 diverged considerably from the wound, and it was suggested in section 6 that this was because the apices of plants 113 and 110, amongst others, had re-united above the levels of insertion of the I_1's, so that I_1 and I_2 arose with their centres further from the wound than usual. Similarly, inspection of the drawings suggests that in apices 113B and 110B, fig. 6, *b* and *c*, the re-union with the other apex of the same plant prevented I_3 from arising just where it would otherwise have arisen—that is, approximately above the wound—and caused it to arise a little closer to the centre of I_1, with the result that its position was unusually close to the position of I_4 and these two leaves were united.

In the remaining four apices I_1 and I_2 converged considerably *towards* the wound, *see* figs. 13, 14, 15, Nos. 123B, 15A, 107A. I_3 and I_4 were joined much more closely, *see* Table III, and they were of the same size and at the same level, whereas in the previous four apices I_3 was distinctly the larger, and probably at a slightly lower level. Consequently in the present four apices the names I_3 and I_4 can only be allotted arbitrarily; but it will be convenient to call I_3 the leaf that arose in the larger angle between I_1 and I_2—that is, on the side above P_1. It may also be noted that in one of these last four apices, No. 71B, I_3 and I_4 had only one axillary bud, which was situated above a point mid-way between their centres. In another, however, No. 15A, each of these leaves had its own axillary bud as usual, while in the remaining two apices no buds were yet visible in their axils.

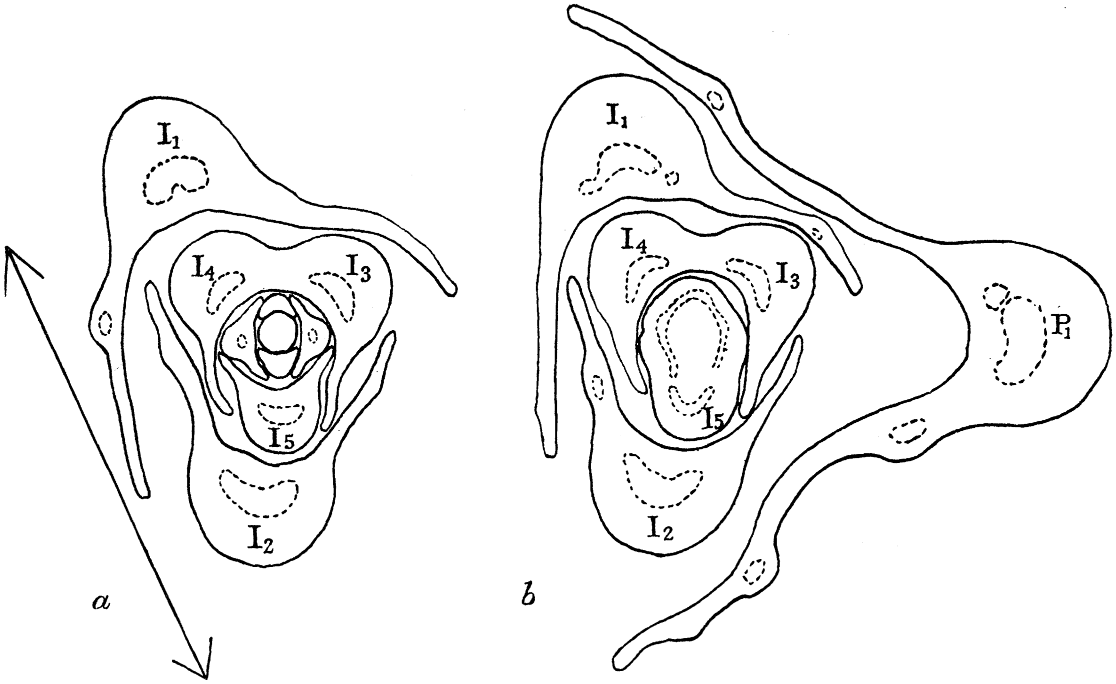

Fig. 14—No. 15A. I_3 and I_4 are closely joined. Sections *a* and *b* at different levels, both × 34

I_3 was again unusually close to the centre of I_1, and the drawings show that, although in all four apices there was a considerable gap between the edges of I_1 and I_2 on the side of the apex above P_1, yet I_3 arose with its centre not quite in this gap, but to one side of it, in the direction of I_1, *see* figs. 13, 14, 15. The explanation is probably that the gap between the edges of I_1 and I_2 was not available for the centre of I_3 because the axillary bud of P_1 reached into it. For this bud could be seen, in these four apices, to be situated directly below or in this gap, and it was probably already present when I_3 was being determined, since in normal apices the axillary bud of the youngest leaf but two is distinctly visible. This explanation is strongly supported by No. 123B, fig. 13, *b*, in which it can be seen that the outer surface of a leaf of the axillary bud of P_1 has united with one side of I_3 ; for this shows that the first rudiment of the axillary bud must have been present before I_3 arose ; moreover, the drawing distinctly suggests that I_3 has been displaced by the axillary bud. Also in one of the smaller pieces formed by the splits, No. 81B, to be mentioned in the next section, the axillary bud of P_1 had united with the apex and had greatly displaced even I_2.

The last four apices, therefore, resemble the previous four in that I_3 arose unusually close to the centre of I_1, though from a different cause. But the position of I_4 in these last four apices was peculiar, for it arose with its centre very close to the centre of I_1—much closer even than the centre of I_3—and it is for this reason that I_3 and I_4 were so closely united. Thus in No. 107A, fig. 15, the divergence angle between the centres of I_1 and I_4 was only 4°, and in the other three apices it was only 21°, 23° and 25°. The angles between the centres of I_3 and I_4 ranged from 54° (in No. 107A) to 93°. Since I_4 was situated obliquely above the central part of I_1, *see* figs. 13, 14, 15, it was clearly situated at a higher level than if it had been in the expected position—that is, in the depression between I_1 and I_2. For this reason, and also because I_4 was united so closely with I_3, it is doubtful whether in these four apices it should be considered as an independent leaf. Instead it may be suggested that one edge of I_3, which was already at rather a high level, had extended over the top of the central part of I_1, and on the farther side had enlarged itself and organized its own vascular strand : indeed in No. 107A, fig. 15, the vascular strands of I_3 and I_4 formed a continuous band. This suggestion is supported by the fact that in both the previous series of experiments on *Lupinus albus* (1931, 1933) it was found that stipules which extended over the tops of wounds were often enlarged on the far sides, while in two apices of *Lupinus albus* a stipule of this kind became completely separate a little way above its insertion (1933, p. 362, and fig. 5). Or if this suggestion is not correct, at least it is probable that in some way or other it was the close union of I_3 and I_4 which made possible the peculiar position of I_4.

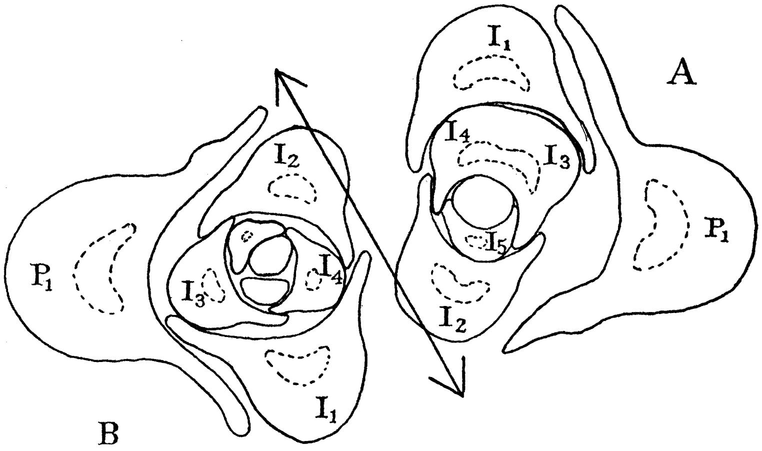

FIG. 15—No. 107, A and B. A has I_3 and I_4 closely joined, B is spiral. × 42

10—The pieces which regenerated incompletely

In twenty of the plants operated on, the split was so far from the median plane that the smaller of the two pieces formed by the split did not regenerate an apex strong enough to grow on indefinitely. Any apex which it may have regenerated formed at most two leaves of about normal size, and was then used up or nearly so. An example was shown in fig. 5, No. 131B, in which two leaves of normal size are present on the smaller piece and the apex above them is so small that it would probably not have grown any more. In another of the smaller pieces, No. 88B, after the first two leaves of normal size three more very small leaves were produced, and then the apex was almost used up.

The chief points of interest concerning these smaller pieces are two. Firstly, in six of them the last leaf formed was a "radial" leaf, having the shape of a long acute cone with a central vascular strand—a structure quite unlike anything found in normal plants of the species. Secondly, the axillary bud of P_1 was usually abnormally *large* in comparison with the axillary bud of the other P_1, and was often spiral or otherwise abnormal in phyllotaxis. The appended Table IV summarizes the development of these smaller pieces. The structures formed, other than the axillary bud of P_1, are called the "regenerate" in order to distinguish them from that bud.

Cross-sections of radial leaves are shown in fig. 16, *b*, *c* and *d*, Nos. 89B, 39B and 58B. In No. 95B, which was left to grow for 27 days, the radial leaf became 7 mm long and resembled in shape a gorse thorn. One reason for considering these radial structures to be leaves is that exactly similar structures were often obtained in another series of experiments on the same species, in which for another purpose P_1 was "isolated"—that is, partially separated from the apex by a vertical tangential cut which left it attached below. For in those experiments when the isolated piece was small, so that it really included only the central part of P_1, it often developed into a quite similar radial leaf. In the present experiments it should be noted that the radial leaves were always the last leaves formed and always used up the apices of the smaller pieces, so that they were nearly terminal in position, though they were situated slightly to one side and grew out obliquely. For this reason, and also because they were much smaller than normal leaves, they seem to have been formed when there was not enough apical tissue remaining to form a normal leaf.

This interpretation is not in conflict with the theory here adopted, according to which a space of a certain minimum size and distance below the growing-point must be present before a new leaf can be determined: for this theory is meant to apply only to the determination of a new leaf at the side of an apex which goes on growing normally. Indeed in previous experiments on *Lupinus albus* in which I_1 or I_2 was isolated from the apex by a vertical cut, the isolated piece of tissue was often found to have been considerably smaller than the normal primary area of I_1 or I_2, and yet it often developed into a small leaf. Since therefore the radial leaves always used up the apex, they may also have been formed from abnormally small pieces of tissue. Their nearly terminal position may also have tended to make them radial.

The leaves I_1 and I_2, when present, occupied the expected positions whether they were normal or radial in form, just as in the apices described already, I_1 arising on the side on which the diagonal cut had left the more room, and I_2 on the other side.

From Table IV it can be seen that in the smaller pieces the axillary bud of P_1 was usually abnormally *large*, and that it was specially large in the pieces contained in group 4 in which the "regenerates" were smallest, and in most of those of group 5 in which there were no regenerates at all. This is at first a little surprising, especially since the pieces of groups 4 and 5 were mostly smaller than those of groups 1, 2 and 3, having been produced by splits that were further from the median plane, as was shown by sections through the bases of the splits. In order to explain this result, we must mention that other experiments on this species, which we hope to report soon, indicate that the determination of an axillary bud is brought about by some influence coming from the subtending leaf. It therefore seems that in these smaller pieces there was in some way a competition between the bud-determining influence of P_1 and the tendency of the apical tissue to regenerate, so that when the apical tissue regenerated very feebly or not at all, the bud-determining influence of P_1 extended over an abnormally large area. Indeed it was often very clear that the bases of the axillary buds of the P_1's occupied tissues which they would not normally have occupied: thus in Nos. 39B and 58B, fig. 16, *c* and *d*, the radial I_1 of the regenerate was situated to one side, and the axillary bud of P_1 extended obliquely forwards and to the other side, so that it took up the remaining tissue which was not taken up by the regenerate. Again, in No. 12B there was no regenerate and the axillary bud extended towards the side on which the diagonal split had left the greatest amount of tissue, its first leaf arising on that side, figs. 16, *a*, and 12, *d*.

TABLE IV—THE DEVELOPMENT OF THE SMALLER PIECES

Numbers of apices	Development of Regenerate	Development of axillary bud of P_1
Group 1. Nos. 88B, 36B, 81B, 131B	I_1 and I_2 of normal form; then apex used up or nearly so.	Enlarged, and decussate or nearly so.
Group 2. No. 20B	I_1 normal, I_2 radial	Enlarged, decussate.
Group 3. Nos. 45B, 49B . .	I_1 normal, no I_2	Much enlarged: decussate in 45B, spiral in 49B.
Group 4. Nos. 4B, 39B, 58B, 73B, 89B, 95B	I_1 radial	Very much enlarged; usually spiral.
Group 5. Nos. 10B, 12B, 15B, 55B, 86B	Nil	Very much enlarged except in 55B and 86B: spiral except in 10B.

Note.—No. 57B did not develop at all, and No. 78B either did not develop or was broken off and lost.

It can also be seen from Table IV that the axillary bud of P_1 was nearly decussate in groups 1 and 2, but usually spiral in groups 3, 4 and 5. Since it was in groups 4 and 5 that this bud usually extended over the largest area, and

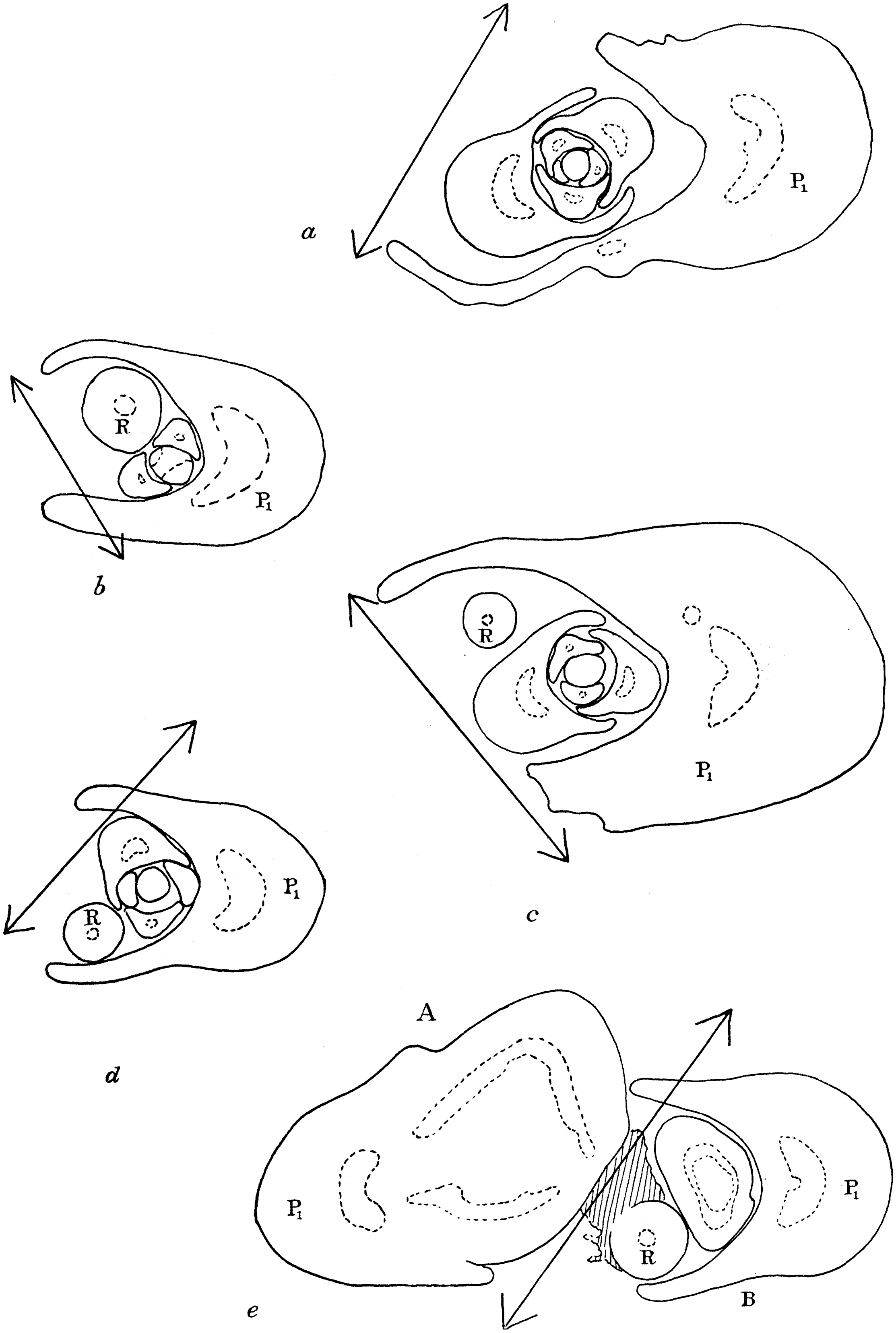

FIG. 16—Five smaller pieces which regenerated incompletely. *a*. No. 12B, showing only a spiral bud in axil of P_1. × 34. (For a section at lower level, see fig. 12, *d*.) *b*, *c* and *d*. Nos. 89B, 39B and 58B, each showing a radial leaf, marked R, and a spiral bud in axil of P_1. *b* × 41, *c* × 46, *d* × 57. *e*. A section through both halves of No. 58 at a lower level. The shaded area represents unorganized tissue. × 44

since this area was usually asymmetric, *see* for instance figs. 16, *e*, and 12, *d*, it can be understood that in these groups the buds were usually spiral. But it does not seem worth while to discuss their phyllotaxis in detail, since firstly, the original shapes of their bases cannot be determined at all exactly, and secondly, WEISSE (1894), has already shown that in many decussate species, spiral *adventitious* buds arise from asymmetric bases. Only one of these buds need be specially mentioned, the bud of No. 10B, fig. 17, which was nearly distichous and had formed four leaves. Its phyllotaxis is explained by the arcs covered by the first three leaves, which all exceeded 180°, as is the rule in the apices of distichous species. The arc of the fourth leaf was nearly 180°.

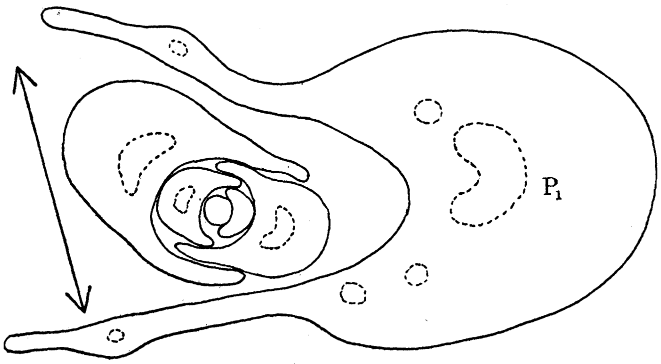

FIG. 17—No. 10B. A nearly distichous bud in the axil of P_1

III—DISCUSSION

It has been shown previously by WEISSE (1894), as was mentioned in section 1, that in species with decussate phyllotaxis adventitious buds, whether produced normally or experimentally, often have spiral phyllotaxis. The present results show further that a shoot apex which is already growing with normal decussate phyllotaxis can be converted by an operation into one (or two) with spiral phyllotaxis. They therefore support the conclusion of WEISSE that the difference between species with decussate and spiral phyllotaxis does not depend entirely (if at all) on any intrinsic difference in the physiological properties of their apices. Moreover, the present results strongly support the opinion of WEISSE (1894), VAN ITERSON (1907) and others, that the difference between decussate and spiral phyllotaxis depends mainly (or entirely) on the manner in which the systems originate, this in turn depending on the arcs covered by the first few leaves formed by the apex and on the shapes and positions of the members below them with which they make contact. For we claim that the development of the various phyllotaxis systems of the regenerated apices has been adequately explained on the basis of the theory that each leaf arises in the first available space, apart from a few points which could not be completely explained since the conditions were not exactly known. These points, which were discussed in sections 6 and 8, were the variations in the angle I_1–I_2, and certain peculiarities in apices 37A and 78A, section 6, and 94B and 16A, section 8.

When the divergence angle between the first two leaves of a regenerated apex (the angle I_1–I_2) was not much above 140°, and when these leaves were inserted at very different levels, so that the system was very asymmetric from the start, then the divergence angles between successive leaves of the subsequent spiral phyllotaxis were fairly constant throughout at about 140°, *see* section 7 and Table I. But when the angle I_1–I_2 was 150° or more, then nearly always the next divergence angle was much below 140°, and the subsequent angles usually (in 13 apices) continued to oscillate regularly above and below the approximate mean value of 140°, even when as many as nine angles were measured. Sometimes, however (in seven apices) the subsequent angles became fairly steady again at about 140°, from the third or fourth angle onwards.

In *Lupinus albus*, which has normally a spiral phyllotaxis, we found previously (1931) that similar oscillations often started after a certain operation—the isolation of P_1 or I_1. For the divergence angle between the next two leaves after the isolated leaf was often much above the normal mean value of 136°, and the next divergence angle was usually well below this value. But the subsequent angles always, or nearly always, became steady at about the normal value. Thus out of 18 series of angles recorded previously in which oscillations started (1931, Table IV, p. 43), in fifteen the series became steady again at the third, fourth or fifth angle, in one, No. 205, it probably became steady at the sixth angle, and in the remaining two, Nos. 132B and 133, it became steady at the seventh angle. (This summary is partly based on some further angles of the same series, which were not published.)

It is therefore clear that in *Lupinus albus* an oscillating series of angles becomes steady again much more easily than in spiral apices of *Epilobium hirsutum*. But it would be premature to conclude that the apex of *Lupinus albus* possesses a special regulating mechanism which brings the angles to a constant value. For it is quite possible that, if the facts were more fully known, this difference between the two species could be explained without any such assumption—perhaps in terms of some such factors as the different shapes and relative sizes of their young leaves and apices. It would be interesting to know how often a constant series of divergence angles is reached by the spiral adventitious buds of normally decussate species, such as those observed by WEISSE (1894).

The question may also be raised whether the shoot apices of decussate species have any peculiarity, not possessed by those of spiral species, which tends to keep their phyllotaxis regularly decussate, provided that it is not too greatly disturbed. WEISSE (1894, pp. 285–6) considers that they do have a peculiarity of this kind. He states that he has examined the apices of many decussate species (not including, however, *Epilobium hirsutum*), and that they have the common characteristic that the youngest pair of leaves grows very rapidly in the radial direction and encroaches upon the apical tissue between them, so that at the end of the first plastochron there remains only a narrow band of apical tissue between them. He considers that this manner of growth tends to keep the phyllotaxis regularly decussate, provided that it is not too greatly disturbed. But our own observations of the normal apex of

Epilobium hirsutum, reported in section 3, do not agree at all with WEISSE's description of the growth of decussate apices. Moreover, it is not clear to us how a manner of growth such as he describes would tend to keep the phyllotaxis regularly decussate. In any case our experiments provide no grounds for supposing that the apex of *Epilobium hirsutum* does have any inherent tendency to return to regular decussation after a slight disturbance. On the contrary, in some of the unregenerated apices, for instance, No. 37B, fig. 9, and No. 16A, fig. 11, the phyllotaxis after the operation differed only slightly from decussation, and yet the differences continued for some plastochrons, in a manner that can readily be understood on the theory here adopted. Also after other operations on the same species, not here reported—especially after isolation of a P_1—the phyllotaxis was often of the kind which was described in section 8 and was called an "oscillating decussation": and even when the oscillations were small, they often continued regularly for several plastochrons. These results seem to us to tell also against the fourth postulate of VAN ITERSON's theory of phyllotaxis (1907, p. 220)—that plants are somehow able to eliminate small irregularities from their phyllotaxis.

Three of the regenerated apices, indeed, which at first were not decussate, did afterwards return nearly to regular decussation, and so also did a few of the "oscillating decussations" which followed the isolation of a P_1. But these returns towards decussation all took place in ways which can be understood on the theory here adopted. An explanation of two of them, in Nos. 94B and 16A, was offered on pp. 80 and 81, and nearly similar explanations will apply to the returns towards decussation after the isolation of a P_1. The way in which the third regenerated apex, No. 15A, returned towards decussation can be understood from fig. 14.

IV—SUMMARY

Apices of shoots of *Epilobium hirsutum* have decussate phyllotaxis—that is, alternating pairs of opposite leaves—until they begin to flower.

Thirty-five such apices were split by vertical cuts in one of the diagonal planes of the phyllotaxis, well before the time of flowering.

Of the 70 pieces of apical tissue formed by the splits, 50 regenerated strongly—growing new apices, and of these new apices 37 immediately developed spiral phyllotaxis, 5 were nearly decussate or became so, and 8 developed a certain other arrangement.

The development of these phyllotaxis systems is explained on the basis of the theory that each leaf arises in the first available space, and the results therefore support this theory.

In 10 of the spiral apices, the divergence angles were fairly constant throughout at about 140°. In 13 others they oscillated regularly above and below this mean value, and in 7 others again they started to oscillate, but quickly became fairly constant.

The remaining 20 pieces of apical tissue regenerated incompletely: they often formed radial terminal leaves and enlarged spiral axillary buds.

The results are discussed, and the divergence angles in the regenerated spiral *Epilobium* apices are compared with those which were found in the apices of *Lupinus albus* after operations reported in a previous paper of this series (Snow and Snow, 1931).

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