THE INTERPETIOLAR INFLORENCENCE OF VINCETOXICUM AND ASCLEPIAS

by

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The peculiar position of the inflorescence in *Vincetoxicum* and *Asclepias,* being at the nodes of the decussate stems between two leaves, somewhat nearer to the petiole of one of them, has for long attracted the attention of botanists.

Indeed ROBERT BROWN in establishing in 1811 the new order of the *Asclepiadeae* characterized them as having "flores subumbellati, fasciculati v. racemosi, interpetiolares" (3). For a good figure representing this particular feature the reader may be referred to a drawing of *Asclepias cornuti* by SCHUMANN (16, p. 462, fig. 122), reproduced by GOEBEL (8, p. 1445).

Notwithstanding the serious attempts by a number of distinguished morphologists, a successful explanation of this remarkable condition has not yet been given. In the present paper the facts will be described first, the description being based on extensive observations on *Vincetoxicum officinale, Cynanchum acutum* and *Asclepias curassavica.* The explanation will be given in the second paragraph, while the third will deal with the literature.

§ 1. The facts.

The flowering region of the stem in our plants is preceded by a decussate vegetative part. In this part the leaves of any pair, though being of equal size themselves, subtend unequal buds. The distribution of these buds is, like in so many analogous cases, a regular one, all strong buds being placed in a dextrorse or sinistrorse spiral with 90° divergence; the weak buds form a homodromous and opposed similar spiral.

In *Vincetoxicum* any internode of the stem shows a conspicuous hair-line, extending from the strong bud of the lower node up to the interpetiolar space of the next higher node. In fig. 1 four successive nodes of a vegetative stem with left winding bud spirals have been represented diagrammatically as A—D. The hair-lines of the internodes being represented by their beginning and ending, each occur twice in two nodes; moreover the fact has been indicated that the buds, when developing, bear a hair-line on their first internode under the prophylls, at the adaxial side.

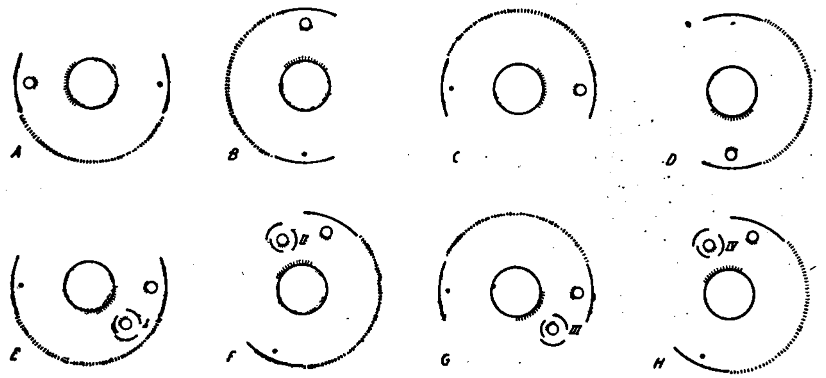

Fig. 1. Empirical diagrams of successive nodes of a flowering stem of *Vincetoxicum* (or *Cynanchum*), A—D being vegetative nodes, E—H flowering nodes. I—IV successive inflorescence peduncles with indication of position of primary bracts.

As soon as flowering sets in, the conditions all of a sudden change in many respects. Fig. 1 E—H represents four successive nodes such as follow on D. The changes are: the rectangular crossing of the leaf pairs is replaced by a skew crossing, in such a way that the third pair falls over the first, and two of the angles between the leaf orthostichies become obtuse, two acute; the latter being for instance 60° to 80°. The bud spirals are replaced by zigzags, the similar buds all occurring in the axils of leaves of the approximating orthostichies.

The inflorescences, being placed in two orthostichies in the obtuse angles, form a similar zigzag, with a divergence of about 140° to 180°. In any node the inflorescence is nearer to the leaf subtending the strong bud than to that with the weak bud; the distance from the former may be about 40° or 50°. The first inflorescence, indicated as I in the figures, is always placed above the angle between the strong buds of the last two vegetative nodes; the second inflorescence II falls over the angle between the weak buds of these nodes.

In *Vincetoxicum* the hair-lines in the flowering part are all directed towards the inflorescences which in their turn have similar hair-lines facing the axis.

Every inflorescence produces three, seldom two, bracts in a spiral order; through the partial overlapping of the third over the first the spiral direction may be determined. Two successive inflorescences are always antidromous and the spiral of the first peduncle is antidromous to that of the bud spirals of the vegetative part.

In *Asclepias curassavica,* where the old long barren pieces of stem through the presence of the different scars yield a very good material for observation, I often observed stems which after a certain flowering period returned to the vegetative condition. When sufficient care is taken not to overlook the scars of small and not fully developed inflorescences, it appears that the return to the vegetative state is governed by very strict rules.

For instance, when the number of flowering nodes between the two vegetative parts is even, be it 2 or 40, the bud spirals are resumed in the same sense and even in the same position, the first strong bud being placed at 90° from the last one of the former vegetative period. In fig. 2 GV represents the beginning of the vegetative part of the stem, such as would follow on the flowering node F. When on the contrary the number of flowering nodes is odd, the new bud spirals are antidromous, and the strong bud spiral starts from a position over the angle between the weak buds of the last two vegetative nodes but one, as represented in fig. 2, HV.

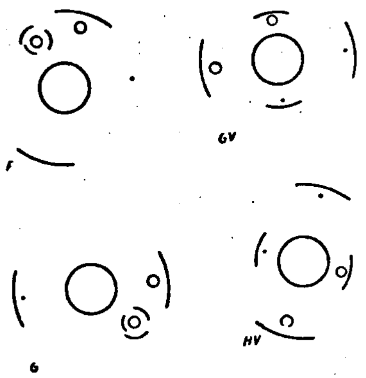

Fig. 2. F and G flowering nodes of *Asclepias,* corresponding to F and G in fig. 1; GV and HV vegetative stem parts such as follow on F and on G.

These are the principal facts. In some cases deviations or complications occur, but the treatment of these may be better postponed until the explanation of the facts has been given.

§ 2. The explanation of the facts and treatment of some abnormal cases or complications.

As maintained earlier (14), the presence of a ¼ bud spiral in decussate stems proves that the leaves have been laid down in a spiral of the main series, from which by metatopy a decussate arrangement has been made. As we shall see this conception not only is confirmed here, but it will even prove to be the key to the understanding of the interpetiolar position of the inflorescence, and the fact that a satisfactory explanation has never been given is only due to the circumstance that the earlier botanists were not aware of the existence of this key.

Our first care therefore has to be to determine which of the two possible alternatives is realized here: are the strong buds from the axils of the older or from those of the younger leaves in the pairs?

In some plants this question may be solved by the presence of mutual approximation of the leaves of a pair. Here such approximation was not to be observed, but the solution was given by the situation of the first inflorescence.

In our fig. 3 the diagrams A 1—E 1 represent the 5 nodes A—E of fig. 1 after the assumption that the oldest leaf of any pair subtends the strong bud. In that case the leaves must have been placed originally as indicated in the diagrams. The diagrams A 2—E 2 on the other hand represent the other assumption that the strong bud is from the youngest leaf.

In both series of diagrams the phyllotactical spiral is antidromous to the bud spirals, as it should be, but the supposed

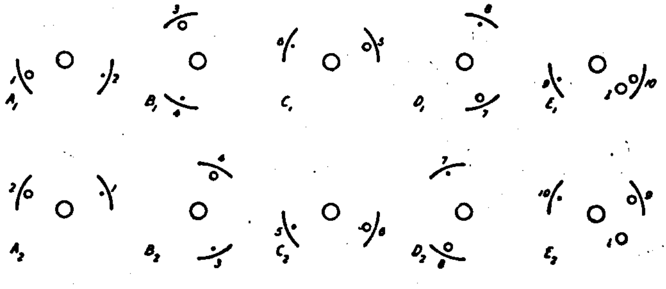

Fig. 3. Theoretical diagrams of nodes A—E of fig. 1, after the supposition that the strong buds are from the first (A_1—E_1) or from the second leaf of the pair (A_2—E_2).

shifts to which the leaves should have been subject before reaching the opposed position are in the reverse sense.

A consideration of the conditions in E 1 soon permits the statement that the strong buds cannot be from the oldest leaves; E 1 does not give a clue to any of the changes in the morphological conditions. In E 2 on the other hand everything becomes natural, when we assume that the inflorescence is terminal, and that it is pushed aside by the strong bud from 10.

In that case the spiral of the weak buds from 1, 3, 5 and 7 is continued by the bud from 9 in the same way, with the only difference that by the transformation of the normal vegetative cone into an inflorescence all buds have grown stronger; in the same way the spiral of the strong buds from 2, 4, 6 and 8 is continued by the extraordinarily strong sympodial bud, a small serial accessory bud having developed before it; in the third place we see that the terminal inflorescence is shifted in a direction more or less opposite leaf 10, not quite, as it is somewhat more remote from leaf 9.

Before discussing this small deviation, we may try to test our explanation by considering a new diagram of node E, made after these suppositions, and represented in fig. 4. Here we clearly recognize, what any actual specimen may confirm, that the phyllotactical spiral of the leaves 1—10 is continued in a natural way by the bracts, which accordingly have been numbered 11—13. And moreover we see that in *Vincetoxicum* the changed position of the hair-lines finds its explanation too, as the hairline of the inflorescence is placed over the strong bud, and that of the strong bud faces its parents axis.

So we may safely infer that in the vegetative part the strong buds are from the youngest leaves, and moreover that the

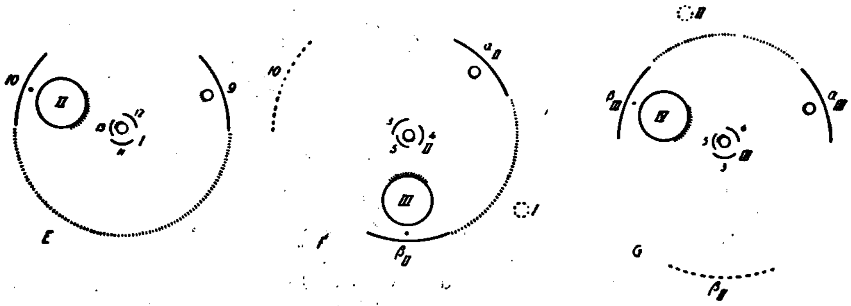

Fig. 4. Theoretical diagrams of nodes E—G of fig. 1.

anomalous position of the inflorescence is due to the original spiral position of the leaves.

If this explanation is correct, we may expect that it may be applied equally well to the conditions of the higher flowering nodes. In fig. 4 there are therefore two of these nodes, F and G, represented in the analogous way. By the aid of these diagrams we recognize that the two leaves of the flowering nodes are the prophylls of the sympodium members; that the position of the peduncle bracts reveals that the phyllotactical spiral runs from α opisthodromously to β, so that the two prophylls must have approached each other at the adaxial side; that the same adaxial approximation of the prophylls is required by the position of inflorescence II, III etc; that the α-prophyll which seems to subtend the strong bud really subtends the weak bud, the β-prophyll subtending the new sympodial member and moreover a small accessory bud; that the inflorescences are not shifted right opposite their subtending leaves, but are somewhat more remote from the α-prophyll, and finally that in *Vincetoxicum* the hair-lines are found in those places which might have been expected from our explanation.

Our views being confirmed in this way, we have still to discuss the question whether the peduncle is not really placed right opposite the original place of the fertile leaf.

In fig. 4 the original position of the leaves has been drawn on the assumption of an original divergence of 135°. In order to bring about the complete opposition of the fertile leaf and the peduncle, the leaves of the pair should have been drawn nearer to each other; to be exact their divergence should have been between 80° and 100°. As divergences in common phyllotactical patterns usually vary between 135° and 144° and a divergence of 80° to 100° is not to be expected here, there must be some special explanation for the actual place of the peduncle.

The pushing aside of the peduncle of course is connected with the change of the normal leaf producing cone into an inflorescence cone forming bracts. Evidently one of the first processes of such a change will be a decrease in the cone area, and a corresponding narrowing of the surrounding zone of the vegetative parts, being in the case of sympodial members the areas of two prospective foliage leaves with the areas of their axillary products.

When these surrounding members, expanding their areas in the normal way for the leaves and to an extraordinary extent for the sympodial bud, intrude upon the apex of the meristematic cone, the inflorescence area may be obliged to concentrate upon one of its excentric parts. In such a way without any further moving the adult peduncle has to assume a lateral position.

Now we may be sure that it is not only the strong sympodial bud which is active in this respect, but a smaller influence may emanate quite well from the small bud, and in the same way the two foliage leaves may have an activity themselves. In any case the final shift of the peduncle may be due to a combination of two influences, one from the strong bud and the fertile leaf, the other from the weak bud and the sterile leaf.

Fig. 5 A represents the case for a sympodial member; the two shifts and their combined effect are drawn as if it was a combination of forces; the two arrows representing the two shifts have been made of such lengths, that their resultant falls 45° from the final lateral position of α.

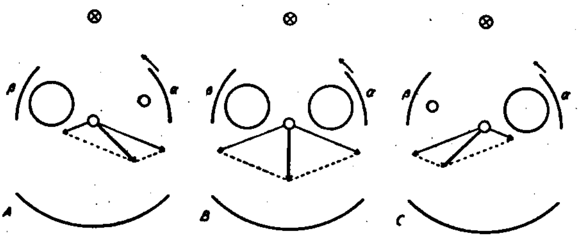

Fig. 5. Representation of shift of terminal inflorescence or of terminal flower by the action of the buds in *Asclepias* and *Vincetoxicum* (A), in *Stellaria media* (B) and in *Lochnera rosea* (C).

Fig. 5 B presents the conditions which are to be expected when the buds from α and from β are equal in force; the final shift is then midway between α and β, but always at the LW-side. This case may be found realized more or less exactly in *Vincetoxicum* in such stems where two strong branches are formed after the first inflorescence formation; it may be found as a rule in many *Caryophyllaceae,* for instance in *Stellaria media,* in the dichasia.

Finally our fig. 5 C gives the case where the α-branch is dominant, as is realized, exactly in the represented form, in the sympodia of *Lochnera rosea,* where the central flower has a lateral position about 45° from β at the LW-side, and the small bud develops as the second flower 1).

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1) For details see my paper appearing soon, on Early binding whorls.

To these three cases in which the reduced terminal cone is shifted towards various parts of the LW-side, might be added two others in which the shift is towards the axil of α or of β; the first is realized in many *Asclepiadeaceae* 2), the second in *Vinca*. In these cases the expansion of the strong bud does not take place at the time when the areas of the two leaves and their axillary products are still at the original places of the spiral arrangement, but later, after the decussate arrangement has become perfect.

No cases are known however in which the shift is towards any part of the SW-side and our explanation will make clear why such shifts are not to be expected.

Our conclusion for the present case of *Asclepias* and *Vincetoxicum* may therefore be that the final interpetiolar position of the inflorescences is wholly explained by the interpretation given above. This having been stated we may discuss some rare deviations and some complications which may be found in certain specimens.

As deviations I can record the development of trimerous foliage leaf whorls, and the occurrence of an abnormal phyllotactical spiral in some sympodium members; as complications we have the often occurring development of supernumerary branches.

1. Trimerous foliage leaf whorls were only observed in my material in one stem of *Cynanchum acutum*, where the highest

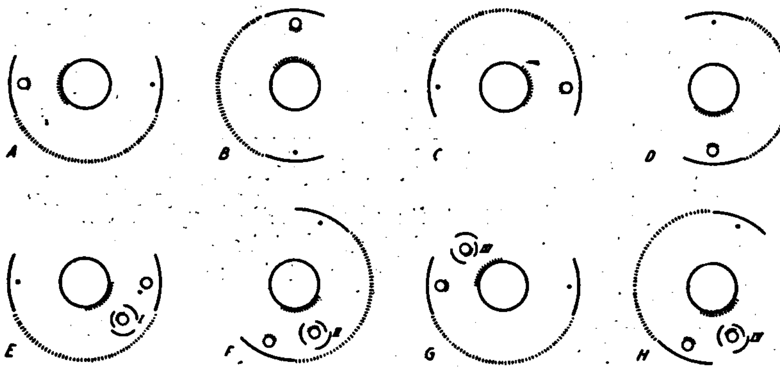

Fig. 6. Particular stem of *Cynanchum acutum* with abnormal phyllotaxis in the first sympodial member, in diagrams of the successive nodes, as in fig. 1.

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2) See below in § 3 sub SCHUMANN.

whorl of the vegetative part and the first sympodial member were both trimerous. For a thorough morphological analysis the specimen was too old, yet it was evident that the three leaves of the sympodial member corresponded to the normal prophylls and the phyllome which otherwise should have been the first bract of the peduncle.

A better analysis remaining desirable, it is clear that the diagrams given in fig. 1 and 4 may have a trimerous variant according to the same rules.

2. The occurrence of an abnormal phyllotactical spiral. This was observed once in *Cynanchum acutum,* where a single stem showed an unusual distribution of the peduncles, the zigzag being disturbed. So this specimen readily attracted the attention. It proved to be regular in all respects (see fig. 6), but for the circumstance that the first sympodial member, though a product of the highest leaf of the vegetative part and antidromous to its parent axis as usual, had its α and β interchanged in position; the spiral consequently ran emprosthodromously from α to β. Through this fact the second peduncle got a position exactly 180° from its normal one and this was the case with all further peduncles.

This deviation evidently does not in the least affect our explanation of the normal case.

3. The development of supernumerary branches.

In *Vincetoxicum* it is not uncommon in the last vegetative whorl of the main axis for the weak bud to develop too, sometimes nearly as strongly as the strong bud. Moreover in the sympodial members the buds from the α-prophylls often develop as weak branches.

In both cases the so-formed branches constitute cincinni of inflorescences, every member arising from a leafy β-prophyll, just as in the normal parts of the plant.

The first member of these cincinni which is an α-branch, is remarkable in the fact that its phyllotactical spiral usually is homodromous to its parent axis, and that its α and β-prophylls seem to be placed without any rule at its right or left side; consequently the spiral runs either emprosthodromously or opisthodromously from α to β, and the first peduncle is turned either to the adaxial or to the abaxial side. So the rare deviation in a β-branch described above is very frequent in α-branches.

§ 3. Literature.

A treatment of the researches and the views of previous authors at the end of the present paper instead of at the beginning, was preferred on account of the rather incoherent character of the literature in question which rendered it extremely difficult to give a clear survey, unless the solution of the problem had been dealt with previously.

The first paper in which an explanation of the interpetiolar position of the inflorescence in *Asclepias* is given, was published exactly a century ago by the brothers Bravais in 1837. In their splendid paper on the inflorescence (2) the authors repeatedly deal with *Asclepias,* and as they quote as species *A. nigra, A. vincetoxicum, A. Syriaca* and *A. tuberosa,* the genus evidently is taken in a very wide sense.

After having described the ramification in the inflorescence itself (p. 321—323) they try to explain the "extrà-axillarité" of the inflorescence (p. 16, 17). They are fully aware of the terminal origin of the inflorescence and of its "déjetement" by the next sympodial member. Moreover they recognize the leafy prophylls as being „géminées", i.e. that they have been laid down with a divergence smaller than 180°, which according to their theoretical views must be 137½° (1, p. 80, 81).

Thus they could have given the full explanation of the interpetiolar position in the sympodial region, if a serious misconception had not prevented them. This was that the skew position must be due to a concrescence of the peduncle with two lateral branches (2, p. 16, 17). Moreover the position of the first peduncle would have remained inexplicable, as the Bravais considered the decussate main stem as having a rectiseriate phyllotaxis.

A valuable observation of theirs is that the extra-axillarity is liable to variation; in *A. Syriaca* they found that the peduncles were placed almost exactly between the two petioles, whereas in *A. tuberosa* they found very little extra-axillarity. They rightly remark that such a variation is proof of the fact that the underlying cause may vary itself, and this is used as an argument for concrescence as being the cause. For us the variation may be explained otherwise, as has been dealt with in the previous paragraph.

Later investigators of *Asclepias* do not seem to have ever noticed these observations and these views, so that this valuable contribution to the solution of the problem has been entirely forgotten.

A different view on the problem has been given by Payer. His full paper never seems to have been published, but the summary has been printed verbatim in the report of the committee, consisting of A. **Richard** and A. **de Saint-Hilaire** (12). **Payer** supposes that every sympodial member (rameau usurpateur) is concrescent with its parent axis up to its two prophylls; the main axis in becoming free at the prophyll level, changes there into the inflorescence.

Our fig. 7, repeating in the upper row the diagrams of the nodes C—G of fig. 1, in the lower row gives a representation of the way in which these nodes should have been constructed after this view. We see that the first sympodial member II, arising from the axil of leaf 8, fuses with its parent axis through one internode; in E the parent axis becomes free in the shape of the first inflorescence and member II fuses with member III which is a bud from the β-prophyll of II.

Though this theory may explain the interpetiolar position of the inflorescences, a closer consideration soon reveals such numerous and such grave objections, that the view becomes entirely untenable. Some of these objections are the following.

In the first place the theory would require that the peduncles should be either inserted exactly between the two petioles as represented in fig. 7, or nearer to the leaf subtending the weak bud; in E the peduncle I might have been displaced towards the left side of the diagram by the approximation of the leaves 7 and 8 on the right, and in F the peduncle II might have been displaced towards the bottom of the diagram by a similar approximation of a and β on the top side in E. The actual position is always the reserve.

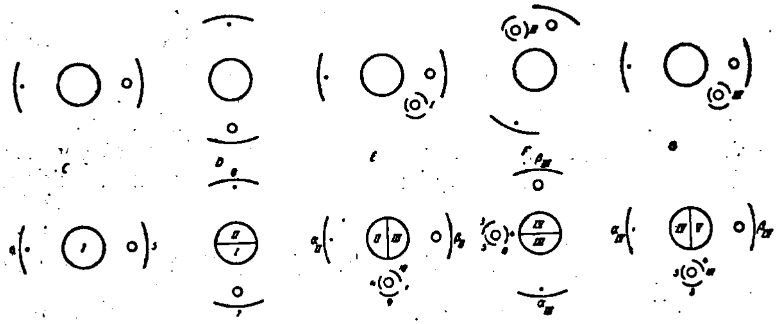

Fig. 7. Upper row: empirical diagrams C—G as in fig. 1; lower row: theoretical diagrams of the same nodes after the concrescence theory of **Payer** and **Eichler**.

In the second place the distribution of the weak and the strong buds would be in contrast to the expectation; in D it would be the second leaf of the node that subtended the strong bud, in C (and all lower vegetative nodes) it would be the first leaf; in E and all higher flowering nodes the fertile leaf β would have not only the strong sympodial bud, but moreover an accessory bud surpassing in size that of the α-prophyll, whereas in D the accessory bud would be smaller than the bud from 7.

In the third place, in those branches from α which have their first peduncle on the adaxial side, or in the similar β-branch represented in our fig. 6 E and F, there would be no explanation for the existence of the first peduncle which would be an axis devoid of prophylls and without a subtending leaf.

The opinion of Payer again has never been taken notice of by any successor; this may partly have been due to the fact that Warming in 1872 erroneously classed Payer with the authors who take the flowering part of the plant as a monopodial system, the inflorescences being lateral branches. Thus it may be explained how Eichler in 1875 independently enounced Payer's theory again.

In 1844 Wichura published his important paper on polarity of buds and leaves (19); notwithstanding his curious starting point from the nature philosophy theory of polarity, he published a number of excellent observations in it. According to Wichura polarity is felt everywhere in nature, in the difference between the two sexes as well as in the complementary colours of double stars, and it is to be observed in buds in the same way.

Buds in the same leaf whorl may be equal, or indifferent, or they may be unequal, or polarized. In dimerous whorls indifferent buds are always opposed, polarized buds may be opposed too, but often they show a lateral approximation (19, p. 185). Amongst the latter group the *Asclepiadaceae* are enumerated (p. 194); Wichura evidently observed in the adult or in the young stages of some form or other an incomplete adjustment of the buds to the decussation, an imperfect metatopy therefore. He even states that in the *Asclepiadaceae* the strong buds are shifted in the anodic direction of the bud spiral, the weak buds being shifted backwards; our fig. 3 will make clear that this observation confirms our statement that the strong buds are from the second leaf of the pair. So his observation yields an excellent confirmation by new facts of the validity of our explanation.

Wichura even understands that the skew shift of the terminal inflorescence is due to the skew position of the strong bud. So

Wichura in fact possessed all the elements for the solution of our problem. But as he believed the decussation of leaves and buds to be an original and real arrangement (once in a controversy with **Wydler** he declared that he had never made any assumption about the genetic order of the leaves in a pair, but always had kept himself strictly to the facts, see 20) the causes of the lateral approximation of the buds remained in the dark and the existence of the two bud spirals itself was only a new and incomprehensible effect of the mysterious polarity; in the same way the morphological phenomena in the sympodial part were all new and independent facts without any apparent reason.

And here again we may state that no botanist ever seems to have noticed the interesting facts described by **Wichura**, and we may add that the unsatisfactory progress since 1844 of the knowledge of our topic is largely due to this circumstance.

In 1850 **Hochstetter** gave a new explanation for the case of *Vincetoxicum*, by supposing that the whole axis, whether flowering or not, is a monopodium, and that the inflorescences are axillary products of the leaves of the next lower node and are concrescent with the main axis, in the way of the flowers in many *Cuphea* spp. (10, p. 183).

We need not to go into details to recognize the error of this view. The supposed adnations are not unlike those postulated by **Payer**, with the difference that for **Payer** the foliage leaves belonged to the axis ending in the inflorescence, whereas for **Hochstetter** the inflorescence axes were devoid of foliage leaves and of prophylls. So the arguments brought forward above against **Payer** in the first and in the third place are at the same time conclusive against **Hochstetter**'s view.

In 1857 **Wydler** wrote a special paper (21) on the inflorescence of *Vincetoxicum* in which he fully described the intricate conditions of the monopodium, the sympodium and the inflorescence parts, in his usual thorough way. He did not quote the works by the **Bravais**' or by **Wichura**, and what is much more remarkable, he did not mention the extra-axillarity of the inflorescences, but dealt with them as if they had been thrown into the axil of the sterile leaf; he wrote (21, p. 5) that the terminal inflorescence is shifted „auf die Seite des fehlenden Zweiges, d.h. des sterilen Blattes, wo sie auf kein Hinderniss trifft". So the problem of the interpetiolar position did not occur to **Wydler**.

Moreover he made a curious mistake by writing that the first sympodial member of the flowering shoot is axillary to the first leaf of the highest leaf pair of the monopodial part, instead of to the second leaf. Evidently this is a slip of the pen: the strong bud spiral of the vegetative part always leads to the first sympodial member. Three years later **Wydler** seems to have been aware of some incongruity in his notations on this point (22, p. 629), without however definitely correcting the error.

The next paper to be quoted is that by **Clos** of 1861 (5). In this paper the author claims for *Vincetoxicum* and for large numbers of other Angiosperms the occurrence of dichotomic branching which is also made responsible for the development of the inflorescences. No morphological analysis and no ontogenetical observations being adduced in favour of this view, the opinion may be passed in silence, the more as the same view, but based on excellent developmental observations, has been enounced in 1872 by **Warming** (18).

Unhappily **Warming** shared the opinion of so many ontogenetists, that the size of the young primordia should be an important item in judging their morphological value. And on finding that in *Vincetoxicum* the young inflorescence, as seen in the first visible stages, is sometimes smaller than the sympodial strong bud, but in other cases is equal to it, he concludes that the branching may be monopodial, the inflorescence being a lateral branch, or it may be due to dichotomy: "Blomsterstanden i nogle Tilfaelde anlaegges som en Sideknop paa Moderaxen (maaske ved Deling af Vaekstpunktet), i andre opstaar ved dennes Kløvning" (18, p. 91).

So we see how even a man of **Warming**'s capacity, instead of studying the works of the **Bravais**', of **Wichura** and of **Wydler** and trying to fill up the gaps in their achievements, contented himself with such fatuous results, under the prejudicial influence of **Schleiden**'s and **Hofmeister**'s developmental method.

This is the more a pity, as **Warming**'s skilful and thorough observations of prepared apices might have led him to a better understanding. In his fine drawings many morphological conditions can easily be recognized and for us it is especially interesting that the shifts are quite or nearly completed at the moment in which the organs become visible.

A particularly good survey is given by his figure 9 on Pl. 7, which for that reason is reproduced here in fig. 8 A. It represents an apex with three inflorescences and part of the vegetative region under them. In fig. 8 B it is repeated in outline, with the notation as given in our own figures; the orientation of the

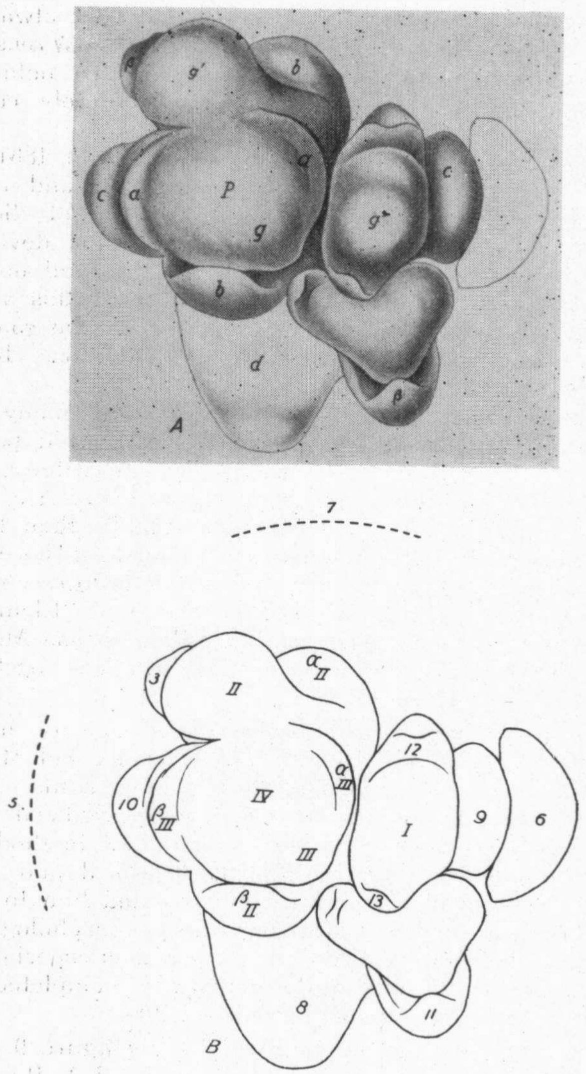

Fig. 8. Apex of flowering shoot of *Vincetoxicum officinale* (A) copied from WARMING (18, tab. VII, fig. 9) and the same in outline (B) with the addition of two missing leaves (in dotted lines) and with symbols according to the explanation given in the present paper.

specimen and the direction of the bud spirals being the same as in fig. 1 to 4, the comparison is easy.

We may recognize in that figure the rectangular crossing of the vegetative leaf pairs (6, 8, 9 and 10); the continuation of the phyllotactical spiral in the bracts (11, 12 and 13 of I, 3 of II); the development of the strong bud in the axil of the second leaf (10, β_{II} and β_{III}); the shift of the inflorescence towards the LW-side and its approximation to the sterile leaf in all three cases; the skew leaf pair crossing in the flowering part by the lateral orientation of the prophylls with respect to the inflorescence; the antidromy of II as compared to I and finally the incomplete metatopy of the prophylls which in II as well as in III are still approached together at the SW-side; all these facts are in good harmony with the explanation given in § 2.

In 1875 EICHLER (7) having reviewed the papers by HOCHSTETTER and WYDLER did not fail to recognize that on the whole WYDLER's explanation is to be preferred, but that the lack of explanation of the interpetiolar position of the inflorescences is a serious deficiency which needs to be supplied.

Trying to fill up this gap, EICHLER without his knowing revived the old explanation given by PAYER 33 years earlier; it goes without saying that it has to be rejected on the same arguments as above.

The weak points in EICHLER's explanation did not escape attention; as early as 1877 it was refuted by CELAKOVSKY (4), on about the same arguments as given in the present paper. One argument, not given here, is that in *Vincetoxicum* the peduncle clearly projects over the insertion of the sterile foliage leaf of the same node, a fact which I can confirm by my own observations.

This precludes the idea that the two leaves of the node might belong to the axis ending in the inflorescence of a higher node: in the lower diagram row of our fig. 7 the inflorescence I might only be inserted higher than the prophylls α_{II} and β_{II} if there were sufficient space between their insertions for a further adnation of I to its daughter axis II, but as soon as I and α_{II} have sufficient breadths to overlap each other, it is I which should have the lower insertion; the facts being the reverse indicate the fault in the theory.

The critical part of CELAKOVSKY's paper being strong, the same is not to be said of all the constructive elements. The best of these is a thorough description of the concrescences occurring in the stems of *Asclepias* (not of *Vincetoxicum*); these adnations are all different from those which the theory of EICHLER should require.

In the second place CELAKOVSKY describes and figures a specimen of *Vincetoxicum officinale* in which the leaves at every vegetative node were inserted at different levels, the second leaves with the strong buds being decidedly higher (4, pl. 1, fig. 3). Evidently this is nothing but an insufficient adaptation to the requirements of decussation.

The most remarkable contribution by CELAKOVSKY is an entirely new explanation of the interpetiolarity of the inflorescence, given on the basis of phytonism of which he was a partisan.

Considering that the terminal inflorescence is pushed aside in the direction of its next higher phyllome (cf. fig. 1, E—H), in the same way as the tendril in *Vitis,* CELAKOVSKY makes a general rule of this relation, and tries to explain it in the following way (4, p. 40).

An axillary bud usually is small in size as compared to the size of the terminal vegetative cone. When the two become equal in size, or when the axillary bud prevails, the terminal cone is shifted in the direction of its most important part, i.e. its first phyton after the subtending leaf.

Against this view we might remark that phytonism is not such a well established theory (cf. 13) that it can be used as an explanatory principle for aberrant morphological phenomena. But we may go farther and contend that the rule established by CELAKOVSKY is not a general one. It is in force for *Vincetoxicum,* as our fig. 5 A confirms. But in *Stellaria media* (fig. 5 B) there is already a notable difference between the direction of the shift of the terminal flower and the position of the first sepal, whereas in *Lochnera* (fig. 5 C) the angle between the two directions is about 90°, and in *Vinca* the angle is even obtuse, the only true rule being that the shift is always to the LW-side.

So the ingenious theory of CELAKOVSKY, by losing its matter-of-fact basis, may be discarded.

After CELAKOVSKY's paper the interest of botanists was hardly ever again directed towards our problem; few authors ever touched on it and if so, it was in a more superficial way.

The next author to be quoted is SCHUMANN, who in 1895 treated the family in the "Natürlichen Pflanzenfamilien" (15, p. 193). His judgment on the question of the interpetiolar inflorescence would not require a discussion here, as it is the usual barren outcome of the view that the observations of developmental stages, however imperfect, are the only and the final truth;

in the present case this amounts to the conclusion that a decision on the monopodial or sympodial branching method of the plant is not to be given, as the actual process really is intermediate between the two modes of branching.

A more important fact is that **Schumann** on account of his vast knowledge of the *Asclepiadaceae* declares that in most genera the inflorescences are borne in the leaf axils, and that if this is so it is in nearly all cases one axil of a pair that produces an inflorescence, the successive inflorescences being placed in a zigzag. Evidently this means that most genera have cincinni of inflorescences in the same way as *Vincetoxicum,* but with the difference that the terminal inflorescence is shifted right into the axil of the sterile leaf on account of the fact that the adaptation to decussation is perfect at the time of the shift.

Our literature survey now leads to a paper of 1922 by **Demeter** (6). Beginning with the remark that a scientific proof for any of the contradictory theories for the arrangement of the inflorescences in the *Asclepiadaceae* has not yet been given, the author states that the solution of the problem has been frustrated by the desire to crowd all forms into one general scheme, and moreover by repeated investigations following one and the same method.

After this promising introduction the paper itself is utterly disappointing. Not only is the old morphological method left alone, but all well established results are neglected too, to such a degree that **Demeter**, though quoting the works of **Wydler** and **Eichler** and pretending to use their notations and symbols, takes the general inflorescence of *Asclepias* as a sympodium from *α* and does not even seem to be aware of a difference from his predecessors. So it is no wonder that the author comes to the conclusion that a study of the *Asclepiadaceae* is insufficient to solve the problem (p. 134) and that only a new method can bring the required light.

This "new" method appears to be comparative morphology, in the shape of a comparison with *Lochnera,* a comparison which had been made already by the **Bravais** brothers in 1837, and which is not very suitable as being a comparison of a cincinnus from *β* with a screw from *α*. The result is that the author, writing: "Es lässt sich das ganze Problem mit einem Schlaglicht erhellen" (p. 137) concludes that the later developmental stages of *Vinca,* by a shortening of the ontogeny, appear already from the beginning in *Asclepias.*

In the last paper to be discussed here, of 1928, **Malme** returns to the view that the interpetiolar inflorescence should be an axillary product (11), but according to MALME the subtending leaf of the inflorescence is not to be sought for on the main axis, but on one of the buds in the axils of the foliage leaves; in the diagrams E—H of our fig. 1 the inflorescences therefore should be lateral axes of the seemingly strong buds, which were taken above as the buds from the first leaves of the whorl.

In itself this view is highly improbable for *Asclepias*. The course of the phyllotactical spiral of the inflorescence, the presence of a normal first pair of lateral leaves in the buds from *a*, prophylls which are inserted far above the inflorescence, already preclude the assumption of such an idea.

It may be worth while however to discuss MALME's arguments, which are not taken from a morphological consideration of *Asclepias* or of *Vincetoxicum*, but from the conditions shown by some South American *Asclepiadaceae*, especially by *Oxypetalum* and *Gonioanthela* in which he describes the presence of two inflorescences at the same node, so that there is no way of taking them both as terminal.

Of course the possibility is not to be denied that in *Oxypetalum* and in *Gonioanthela* the succession of cormi may be entirely different from that in *Asclepias*, though the statement of SCHUMANN (15) about the uniformity of the arrangement of the inflorescences in the family is not favourable to such a view.

Unfortunately MALME does not give a detailed morphological analysis of any of the described forms, and his diagrams are not constructed in a satisfactory way. So we are not informed about the spatial relations between the inflorescences of successive nodes, nor about the position of the bracts on the inflorescence peduncles. The only thing we learn is that the two inflorescences are borne at both sides of a single one of the two buds of the whorl.

It was for this reason that I tried to get some supplementary information by a study of some of the forms described by MALME, or some related forms. For this purpose some specimens were examined from the Groningen Herbarium, namely *Roulinia Jacquinii* and *Oxypetalum riparium*.

Roulinia Jacquinii Decne (leg. C. A. PURPUS 1909, Rio de San Francisco, Puebla) was chosen because MALME reports that *R. montevidensis* often has two inflorescences at the base of the bud from one of the leaves. On examination of a soaked specimen its succession of cormi proved to be essentially the same as in *Vincetoxicum*, even the hair-lines on the adaxial side of the branches in the flowering part and in the peduncle at the side facing the β-branch being present and greatly facilitating the examination.

The sympodium was formed by the strong branches from β; the sympodial members all being antidromous to their parent axes, the successive main peduncles were distributed in a zigzag.

The accessory buds in front of the β-branches usually were developed into small branches with nothing but two small vegetative leaves.

The buds from α mostly developed into weak sympodia, with an inflorescence at every node. In the higher parts of the sympodia they were reduced to a single pair of leaves and one terminal inflorescence, and these may easily have been mistaken by MALME for the second inflorescence of the big node; the main inflorescence falling near the α-prophyll it was always very near to the terminal inflorescence of the α-branch.

Oxypetalum riparium H. B. K. (leg. C. A. PURPUS, Aug. 1912, Misanila, Veracruz) was intended to illustrate the conditions of the genus of which MALME examined four species. Our species but for the absence of hair-lines, showed the same conditions as *Roulinia;* there were strong sympodial and antidromous β-branches, ending in inflorescences placed in a zigzag; in one case it was even possible, notwithstanding the disadvantages of herbarium material, to determine the position of the first peduncle bract which was as it should have been. The accessory buds in front of the β-branches did not develop, though being quite distinct buds; the α-branches produced weak sympodia which when poor may have been mistaken for the second inflorescence.

Our conclusion therefore is that the explanation given by MALME is wrong in any case for *Asclepias* and for *Vincetoxicum,* and that it is unlikely that it will be right for any member of the family, the succession of cormi in which seems to follow one and the same scheme throughout.

These are the principal papers touching our topic. Others might have been discussed, but as they did not bring new facts or new constructive views, they were omitted; thus for instance VELENOVSKY who again defended EICHLER's view (17, p. 614) or GOEBEL who connected the inflorescence zigzag with an oscillating symmetry (9, p. 35).

§ 4. Summary.

1. The interpetiolar inflorescences of *Vincetoxicum, Asclepias* and other genera of the *Asclepiadaceae,* as well as the seemingly

axillar inflorescences of many other *Asclepiadaceae* are all terminal to the main axis or to short members of the sympodial axis. Every sympodium member consists of a thick basal stem part with leafy prophylls, usually two in number, taking part in the construction of the sympodium, and a thinner terminal inflorescence which is pushed aside by the basal part of the next sympodium member. The first sympodium member arises in the axil of the highest leaf of the last vegetative whorl of the vegetative axis, all subsequent sympodial members being borne in the axils of the β-prophylls.

2. The interpetiolarity (or extra-axillarity) of the inflorescence, where present, is a consequence of the fact that the stem originally has a spiral phyllotaxis from which by means of metatopy a decussate arrangement is formed. The failure of the old morphological school to explain the interpetiolarity is due to the circumstance that this school used to consider the decussation as an original phyllotaxis. In consequence of this lack of success even the well established results have been ignored by modern botanists, who rarely attacked the problem and who, when they did, entirely lost the way.

3. The two highest vegetative leaves of a stem or the two leafy prophylls of a sympodium member having been formed in a spiral position, we may distinguish in the dimerous whorl between an SW (short way)-side and an LW-side. The inflorescence being pushed aside very early by the strong bud from the second leaf, is shifted towards the opposite side. When the strong bud at the time of its expansion activity is still placed more or less in the position based on the spiral phyllotaxis, the inflorescence is pushed towards the LW-side, in the vicinity of the sterile leaf.

4. Besides the expanding influence emanating from the strong bud, there may be similar influences from the weak bud and perhaps from the leaves. Consequently the actual shift direction may be the resultant of a combined action. Actually the divergence between the inflorescence and the sterile leaf which without this combination might not exceed some 20°, often may be higher, up to 60°.

5. If at the time of the crowding aside the metatopic changes have already been completed, the inflorescence is thrown right into the axil of the sterile leaf and consequently there is no interpetiolarity. This condition is realized in many *Asclepiadaceae*.

6. The sympodial members are always antidromous to their parent axes. They moreover nearly always have their α-prophyll

on their right when their spiral is right-handed and reversely, so that the spiral from α runs opisthodromously towards β. As a consequence the successive inflorescences are placed in two orthostichies in a zigzag. Another consequence is that the spiral arrangement of the strong buds and of the weak buds of the vegetative region is replaced by a zigzag arrangement. As the prophylls of any sympodial member are placed laterally with respect to the inflorescence, the rectangular crossing of the vegetative leaf pairs is replaced by a skew crossing, the angle of which is determined by the degree of extra-axillarity of the inflorescence.

7. In some cases a flowering sympodium may grow out again into a vegetative axis. In such a case the phyllotaxis of this vegetative axis, apart from the metatopies, is the same as that which the next sympodial flowering member should have had.

8. The circumstance that these different morphological phenomena are all readily explained by the assumption of a spiral origin of the decussate phyllotaxis, is a new proof for the validity of such an assumption.

9. Branches from α-prophylls usually are homodromous to their parent axes. As the position of α and β is not fixed beforehand, the spiral may be opisthodromous or emprosthodromous.

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