ON WHORLED PHYLLOTAXIS.

IV. EARLY BINDING WHORLS [1]

by

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(With Tab. XIII).

CONTENTS.

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[1] For preliminary communications on part of the contents of the present paper see 48 of literature list and: "Over de dorsiventrale dekussatie van Paronychia en Herniaria", Nederl. Kruidk. Archief 46, 1936, p. 477. See moreover 53 of literature list on a nearly related topic.

CHAPTER 1. INTRODUCTION.

§ 1. What early binding whorls are.

In the second paper of this series (47, p. 129) those false whorls have been termed binding whorls in which the separate leaf primordia of any phyllotactical system are attached to their lateral neighbours and are more or less firmly united to them, so that on the elongating stem the cohering leaves will seem to be placed in a whorl.

The class of binding whorls is very extensive (47, p. 168) and embraces the overwhelming majority of plants with typical vegetative whorls such as *Equisetineae, Casuarinaceae, Labiatae* etc (51); no doubt these plants usually derive a biological advantage of some kind or other from the whorled condition.

About the process of binding which is of an unknown nature, we may say that it takes place in the stem, not in the free leaf parts. Whenever a connation of leaf bases follows, as is the case in *Dipsacus*, this is only a secondary complication, a non-essential addition, rendered possible by the false whorl formation.

In the second place we may state that the binding may take place at different developmental stages.

In *Peperomia* we met with a case (47) in which the binding occurs late and is so imperfect that the original spiral phyllotaxis is hardly obscured. Usually however the binding occurs early, even so early that the first visible stages of the leaf primordia are perfectly whorled, and the adult whorls are not to be distinguished from true whorls; these forms are called early binding whorls here.

In the present paper a number of plants with early binding whorls will be dealt with.

§ 2. The phyllotactical patterns from which binding whorls are formed.

The most important question to be dealt with in the present chapter is how we may get any knowledge about the phyllotactical system from which a certain binding whorl is formed.

On considering that beyond false whorls the Angiosperms hardly ever show any other systems but those of the main series, the rare exceptions being systems of the first accessory series or other anomalous series, we may expect beforehand that in nearly all cases the binding whorl is a transformed system of the same main series.

The same conclusion is to be derived from a study of the phenomena in biastrepsis. For as expounded earlier (51, p. 673) biastrepsis is due to the action of the same binding process which acts in binding whorls, the binding order only being different.

Now as the abnormal order is derived from the original pattern just as is the normal order in binding whorls, we may get some additional knowledge from it about the original arrangement, and as we shall see below, this nearly always points to an underlying system of the main series.

About the direction and the course of the spiral in the normal specimens without biastrepsis this method does not give any information, but such a knowledge may be often derived from two other sets of rather frequent phenomena, namely by imperfections of the whorl formation and from the discontinuation of the whorl forming factors in a higher region of the shoot, and moreover in a few cases from the progressive metamorphosis of the whorl members.

We shall therefore successively deal with these sources of information, in a general way.

1. Biastrepsis. The cause of biastrepsis is always that the binding instead of uniting the leaves into rings, forms a single spiral band out of them.

In this spiral band the leaves of the successive coils are nearly always placed alternately, any leaf lying above the space between two lower leaves. So the spiral constitutes a secondary pattern of the form m + (m + 1), in the same way as the whorls are secondary patterns m + m.

In plants where the normal shoots are decussate, the secondary pattern in biastrepsis shoots always seems to be 2 + 3; at least no other cases have come to my knowledge. Of course the twist to which many biastrepsis shoots are subject, in consequence of the unrolling of the spiral band during the elongation of the shoot, seemingly gives the appearance that the coils of the spiral are set with a much greater number of leaves than 2 or 3, but the real state of things can easily be discovered by following the stem surface lines which indicate the originally longitudinal cell rows of the epidermis. DE VRIES was the first to realize that in such a way the phyllotactical pattern of the shoot may be determined (62), and he found that the decurrent fibres from the midrib of any leaf *n* pass between the insertions of the leaves *n*-2 and *n*-3 in shoots with biastrepsis of *Valeriana officinalis* (63a, p. 151), *Saponaria officinalis* (p. 153), *Galium Aparine* (p. 155), *Guizotia oleifera* (p. 161) and *Collinsia canadensis* (p. 162), the secondary pattern in these specimens being therefore 2 + 3.

DE VRIES moreover tried to determine the exact divergence of the original system, and finding in *Guizotia* that the leaf midrib fibre, when traced lower down, led to leaf *n-13*, he concluded that there was an original divergence of 5/13; the same divergence was found in the other species quoted above, in *Rubia tinctorum* (62, p. 88) and in *Dipsacus* (63, p. 25). In my opinion these conclusions are not warranted, as even in plants without any binding or biastrepsis the leaf-traces, fibres and surface lines may diverge from the longitudinal course (46, Ch. 7, p. 283).

Yet these fine observations establish beyond doubt that in all these twisted stems the phyllotaxis is a system of the main series with binding after the SW spiral ¹). The same follows

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¹) ZIMMERMANN contends (86, p. 272) that for *Dipsacus silvestris* DE VRIES has shown that the spiral arrangement is due to the inactivation of the factors for the rhythmic shortening of the internodes and for the rhythmic differentiation of the divergences.

DE VRIES however nowhere enounced such a view and only correctly stated that any twisted shoot has a spiral phyllotaxis, either by a sudden transition from the whorled condition, or in some laterals from the beginning (63, p. 87); the description given by ZIMMERMANN clashes with the facts, as a shoot with biastrepsis is not a transformed decussate shoot, biastrepsis and decussation both being equivalent transformations of a spiral system.

for *Stachys palustris* from the observations of NESTLER and SCHIFFNER (39, p. 130).

In proof of the above view we may refer to our fig. 1 in which some possible ways of spiral binding in a system of the main series have been represented. Fig. 1 *A* illustrates a binding after the LW genetic spiral. In such a system the surface lines

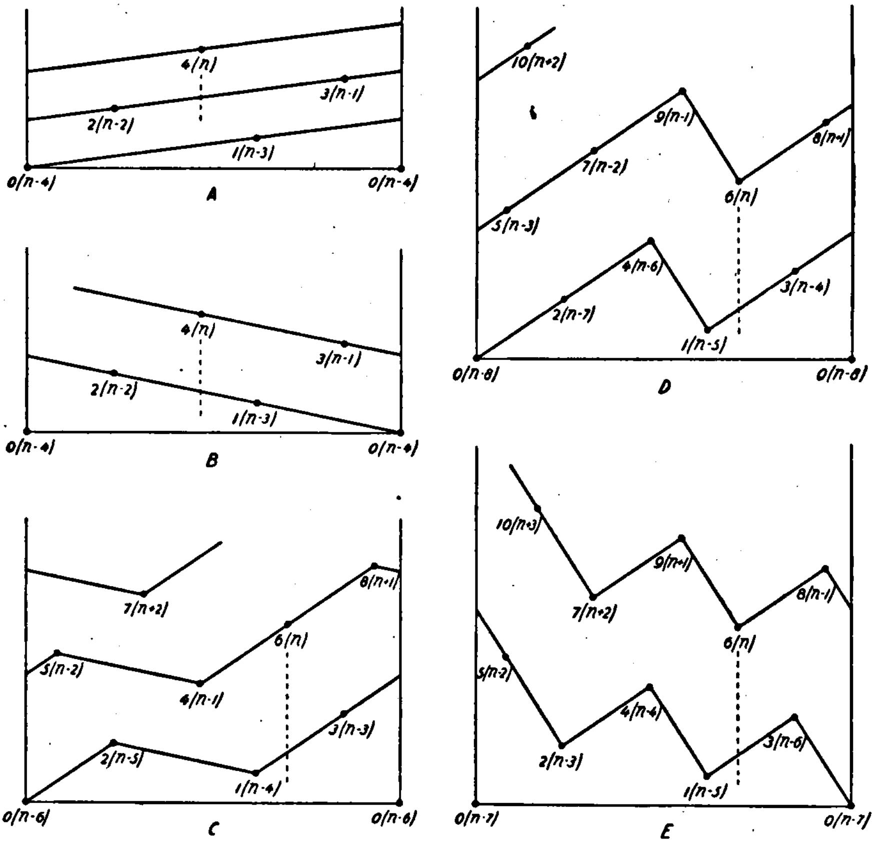

Fig. 1. Schematic representation of some simple biastrepsis binding patterns, formed in systems of the main series. Leaf centres numbered according to their genetic order, and moreover (in brackets) according to their distance from an arbitrarily chosen higher leaf *n* in the winding spiral (= the continuous line).

The secondary patterns are 1 + 2 (*A*), 2 + 3 (*B*), 3 + 4 (*C*), 4 + 5 (*D*) and 5 + 6 (*E*); the traces of leaf *n* (dotted lines) consequently pass between the insertions of leaf *n*—1 and *n*—2 in *A*, between *n*—2 and *n*—3 in *B*, and so on.

from a leaf *n* pass between the lower leaves *n*-1 and *n*-2; the secondary system consequently is 1 + 2. This case has never been reported as far as I know.

Fig. 1 *B* is the usual secondary pattern 2 + 3, with binding after the SW genetic spiral. In fig. 1 *C* - *E* three other patterns have been drawn, with secondary systems 3 + 4,4 + 5 and 5 + 6. But it will be clear that 3 + 4 might also have been realized in a system from the first accessory series, and *D* and *E* might even be due to a binding in a great number of ways in different original systems.

The secondary systems 1 + 2 and 2 + 3 on the other hand are only to be derived from the main series, and the fact, that 2 + 3 is so very common, indicates therefore that the secondary patterns in otherwise decussate plants are transformations from the same original system as the normal dimerous whorls; this result in itself tends to confirm the validity of our conclusions.

In plants with normally polymerous binding whorls the biastrepsis shoots, when developed, have coils with a larger number of leaves and secondary patterns m + (m + 1), with higher values of m.

The analysis of such secondary patterns is not only impeded or frustrated by the circumstance that a number of theoretical derivations may be imagined, but moreover by the fact that, in the same way as the whorls in the normal shoots are often heteromerous as soon as the whorl number is elevated, the alternation in the coils of the spiral band is disturbed, so that the secondary spiral is no longer regular.

This was observed in a biastrepsis shoot of *Hippuris vulgaris,* a specimen represented in fig. 2, as seen from three sides.

The base of the shoot had seven regular whorls of 11, 11, 11, 9, 9, 9, 8 leaves, followed by several irregular and imperfect pieces of whorls and of spirals; then came the drawn part, with one whorl of 7 and an incomplete whorl of 6 leaves, followed by a regular spiral of which 15 coils might be counted. For the purpose of drawing most leaves in the specimen were cut.

In the specimen it is evident that a slight twist has taken place. The dotted lines represent the course of the long air-spaces in the cortex, which in normal shoots run vertically up and down.

When we determine by means of these air-spaces to which part of the spiral band the traces of a leaf *n* lead, we come to the conclusion that this varies in the different parts of the specimen; the trace may abut on leaf *n-7* (leaf 71 leads tot 64), it may pass between leaf *n-6* and *n-7* (e.g. leaf 63) or between *n-7* and *n-8* (e.g. leaf 48). Such a relation corresponds exactly with the fact that the normal whorls are always heteromerous; evidently both the whorl binding and the spiral binding are

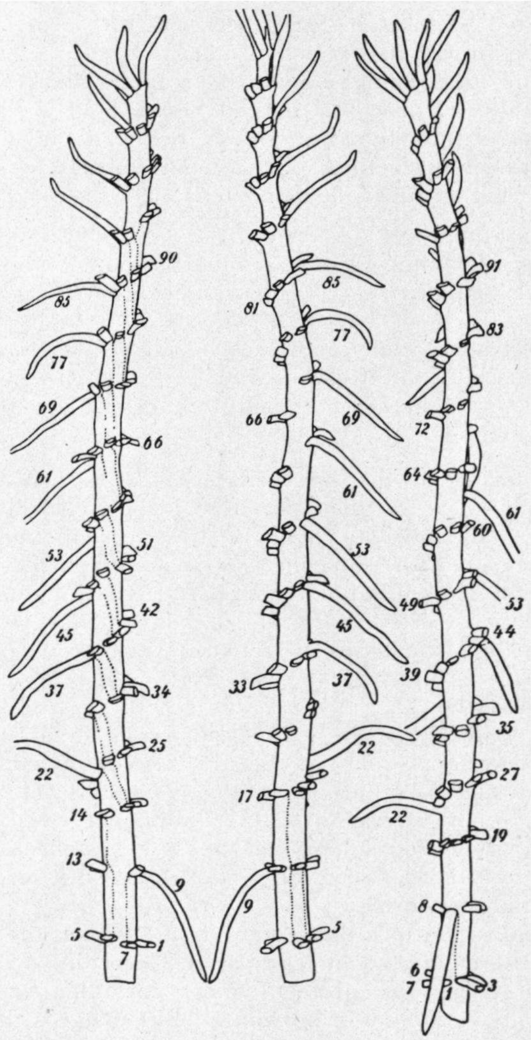

Fig. 2. *Hippuris vulgaris*, shoot with biastrepsis, drawn from three sides, × 2.

not formed in a regular scheme, but are subject to many variations.

A further analysis of the twisted or the normal shoots in *Hippuris* is rendered impossible by the fact that the shoot is unlimited, and consequently continues its binding to the very end. The only thing we learn is that whorls and binding spiral are constructed on the same principles and this is in itself a gain.

2. Imperfections of the whorl formation.

The binding itself being sometimes irregular in its distribution and all changes required for the conversion of a primary phyllotactical pattern into binding whorls being liable to a partial realization, the imperfections of the whorl formation may consist of the following groups of phenomena.

a. Irregular binding;
b. imperfect levelling of the members of one whorl;
c. imperfect equalizing of the angles between the whorl members;
d. imperfect adaptation of successive whorls to a regular junction, usually to alternation;
e. imperfect elimination of the differences in age between the whorl members.

Before entering in the next chapter into a consideration of the numerous facts of these kinds which are to observed in nature, we shall have to deal in this introduction with the characteristics of such imperfections to be expected in binding whorls formed from phyllotactical patterns belonging to different phyllotactical series. For sake of convenience we shall successively consider the cases of dimerous, trimerous, tetramerous and pentamerous binding whorls.

a. Dimerous whorls.

Dimerous whorls may be formed in low systems of the main series. High systems such as $8+13$ are excluded, the space between two successive leaves in the genetic spiral being quite taken up by other leaves, so that a binding between leaf n and leaf $n+1$ is rendered impossible; in low systems as $1+2$ or $2+3$ a connection between any two successive leaves on the other hand may be formed.

For the realization of a dimerous binding whorl, the two leaves of a pair must be united on both sides, according to a LW and a SW divergence; for perfect whorl formation the changes enumerated above include a horizontal shift towards the LW side.

These shifts for divergences between 135° and 144° amount to values from 22.5° to 18°. Supposing that in any system of the main series perfect dimerous whorls have been formed, and that they have been rendered alternating by a torsion of the stem so as to change the mean divergence into 135°, the system may be represented by our fig. 3. As we see, the original genetic spiral has been converted into a broken line, and the divergences along it are successively 180°, 90°, 180°, 90° etc; it may be designated by the formula $(180° + 90°) : 2 = 135°$.

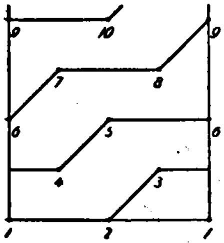

Fig. 3. Diagram of dimerous binding whorls, realized in a system of the main series. Continuous line = transformed SW genetic spiral.

The lower members in the successive whorls form a ¼ spiral which is antidromous to the genetic spiral, and this is also the case with the higher members. Hence we may conclude that if any one of the whorl forming processes shows some deficiency, the result will be that these two antidromous ¼ spirals will appear; in the following chapters numerous examples of such a condition will be described.

As expounded earlier (Schoute 47, p. 138) dimerous binding in the main series is to be expected in the case where the binding of the primordia favours the LW and the SW spirals. In these cases leaves 1 and 2, being older than leaf 3, will unite on both sides.

Nearly all other series with spiral systems are not appropriate for the formation of dimerous binding whorls, as the difference between the LW and the SW divergences is too great.

In low systems of the series 2, 2, 4, the first jugate series, on the other hand dimerous whorls are present without any binding and without any metatopy.

So if really, as is generally held, the systems of this series occur in the *Dipsaceae,* their dimerous whorls of foliage leaves should be mentioned here. The action of binding, which is not required for the formation of dimerous whorls in this series, is evidently active in the *Dipsaceae,* as is proved by the frequently occurring cases of biastrepsis.

b. Trimerous whorls.

In most cases trimerous whorls are formed out of low systems of the main series, in the way indicated in fig. 4 *A;* the divergences of the original genetic spiral are changed into a regular succession of 120°, 120°, 180° after the formula $(120° + 120° + 180°) : 3 = 140°$.

This is realized when the binding prefers the SW genetic spiral and the binary parastichies. Here all deficiencies in the whorl formation must produce phenomena distributed after a homodromous ternary parastichy, as the lower, middle and upper members of the consecutive whorls are all placed in such parastichies.

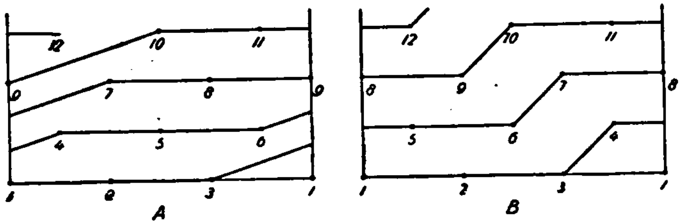

Fig. 4. Diagrams of trimerous binding whorls, *A* realized in a system of the main series, *B* in one of the first accessory series. Continuous lines = transformed SW genetic spirals.

In other cases trimerous whorls may be formed out of low systems of the first accessory series 1, 3, 4, 7....; these whorls are represented schematically in fig. 4*B*. Deficiencies in the whorl forming must betray themselves by phenomena arranged in an antidromous ternary parastichy, as fig. 4*B* illustrates sufficiently; the formula is $(120° + 120° + 60°) : 3 = 100°$.

In § 24 on *Helianthus* clear instances of these two kinds of trimerous whorls will be dealt with.

Theoretically trimerous whorls might arise also from systems of the trijugate series 3, 3, 6, .., but no instances can be given.

c. Tetramerous whorls.

In systems of the main series tetramerous whorls may arise (cf. Schoute 47, p. 149) if the binding prefers the binary parastichies, and is moreover possible along the SW genetic spiral, and if no other way is possible, after a ternary parastichy.

If perfect and alternating, they assume the form given in fig. 5*A*, the formula of which is $(180° + 90° + 180° + 135°) : 4 = 146\frac{1}{4}°$. All consequences of imperfections of the whorl formation must be distributed in an antidromous $\frac{3}{8}$ parastichy, as a glance at the figure shows. A good case will be dealt with below in § 19 on *Casuarina*.

In other cases tetramerous whorls may take their origin

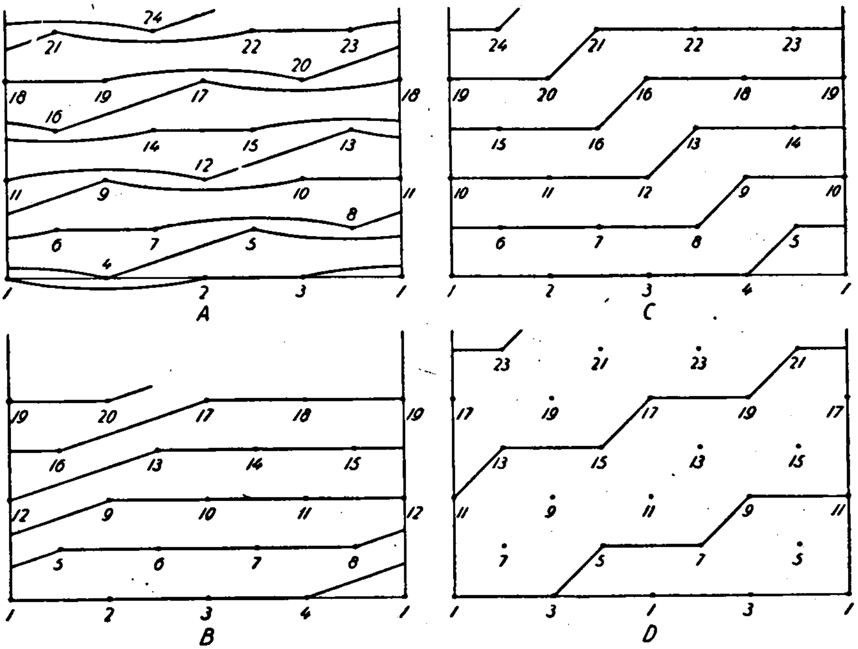

Fig. 5. Diagrams of tetramerous binding whorls, *A* realized in a system of the main series, *B* in one of the first, *C* in one of the second accessory series, *D* in one of the first jugate series. Continuous lines = transformed genetic spirals.

from the first or from the second accessory series 1, 3, 4 and 1, 4, 5; fig. 5*B* and 5*C* illustrate these cases. Their formulae are $(90^\circ + 90^\circ + 90^\circ + 135^\circ) : 4 = 101\frac{1}{4}^\circ$ and $(90^\circ + 90^\circ + 90^\circ + 45^\circ) : 4 = 78\frac{3}{4}^\circ$.

All morphological phenomena due to imperfections in the whorl forming must be arranged in these cases in a $\frac{1}{8}$ spiral, a spiral which is homodromous with the genetic spiral in the first and antidromous to it in the second accessory series. Instances of both will be described in *Helianthus*.

In the fourth place tetramerous whorls may be formed from systems of the first jugate series 2, 4, 6. Fig. 5*D* gives such a case; in the figure only one of the two original binary parastichies has been indicated by a drawn line.

In whorled systems of this description imperfections of the whorl formation might reveal that in any whorl, there are two originally lower and two originally higher members, and that the homologous members are arranged in a $\frac{1}{8}$ spiral which is antidromous to the binary parastichies.

A few, and moreover not very distinctly developed, instances will be described for *Helianthus*.

d. Pentamerous whorls.

From systems of the main series pentamerous whorls will be formed when the binding prefers the binary and the ternary parastichies (SCHOUTE 47, p. 150); if perfectly realized and alternating, they assume the form of fig. 6. The genetic spiral has been transformed according to the formula $(144^\circ + 144^\circ + 144^\circ + 144^\circ + 108^\circ) : 5 = 136.8^\circ$. All phenomena due to deficiencies of the whorl formation must ascend in antidromous 1/5 spirals, as fig. 6 will make clear; instances have been described earlier for *Peperomia* (47, p. 151).

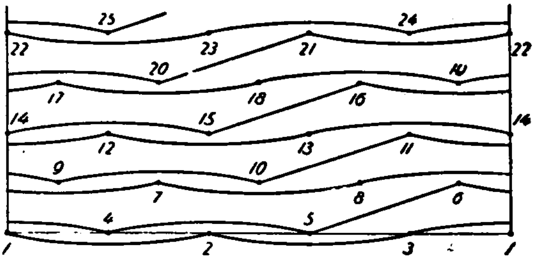

Fig. 6. Diagram of pentamerous binding whorls, realized in a system of the main series. Continuous line = transformed SW genetic spiral.

Other phyllotactical series from which pentamerous binding whorls might take their origin are the second and third accessory series 1, 4, 5 and 1, 5, 6; instances however have not come to my knowledge. In both cases the phenomena would be arranged in 1/10 spirals, being antidromous for 1, 4, 5 and homodromous for 1, 5, 6.

The only author who ever gave similar theoretical derivations of whorls from spiral systems was VON NAEGELI (38, p. 486). In a number of cases his formulae, though somewhat more complicated, amount to the same as those given above; in other cases he omitted formulae given here, or conversily gave such which are not taken into account above.

The limitation of the number of his formulae was due to the circumstance that VON NAEGELI did not pay attention to the existence of different series of phyllotactical patterns, but arbitrarily derived his whorled systems from spiral systems with divergences varying between 100° and 180°. So the series 1, 4, 5 for instance fell outside his consideration.

On the other hand von Naegeli admitted the possibility that isomerous whorls might have two different modes of junction, alternating in a predestined manner; for the case of trimerous whorls for instance the successive divergences might be 120°, 120°, 180°, 120°, 120°, 60° and so on, giving a mean divergence of 120°, a value therefore which in itself is highly improbable (cf. Schoute 46, p. 298).

Though it is not to be denied that in such cases where the original divergence differs too much from the required value, the junction of two particular whorls occasionally may be anomalous to obtain regular and alternating whorls, it does not seem probable that a regular alternation of the mode of junction may be realized; in any case no facts have been reported pointing in that direction.

The above theoretical considerations enable us to compare the actual facts with the expectations. Whenever we find that peculiar morphological characteristics in certain whorls are distributed in a way corresponding to what has been described here for a certain phyllotactical series, we may conclude that the shoot in question originally had a pattern of that series. And when we have other means of checking that original pattern, and especially when we are able to determine the direction and course of a genetic spiral in it, we may subject our general views to a severe test. As we shall see no disagreement was ever met with in any object.

3. Regional whorl forming.

The binding phenomena, being incorporated into the developmental processes of the leaves, are often restricted to a certain leaf category, e.g. to the foliage leaves.

A shoot producing successively leaves of different plastics may be whorled in one or two regions only (comp. 47, p. 164, 51, p. 673). From the other regions where the original pattern is to be observed unaltered, the direction and course of the genetic spiral may be traced into the whorled part.

Cases in which a spiral part is followed by binding whorls are very rare; those in which a spiral region comes after a whorled one are frequent. Common cases are whorled shoots with terminal flowers in which an imbricate calyx is to be observed, and further, whorled shoots with spiral bracts in a terminal inflorescence. Other plants have only the lower foliage leaves in whorls, the higher losing their binding gradually.

These discontinued whorls may offer excellent material for the observation of the mode of conversion of the original phyllotaxis into binding whorls.

4. Progressive metamorphosis.

In such cases where the binding whorl formation is not restricted to a certain leaf category but comprises two or more successive different leaf forms, the progressive metamorphosis of the whorl members according to their order in the original spiral may betray the course of the latter in a very instructive way.

Two such cases have already been described for the late binding whorls of *Peperomia* (47), namely that to be observed in the transition from the rudimentary subterranean leaves to the much larger foliage leaves (l. c. p. 141; see also fig. 7 and 8), and further the transition from the foliage leaves to the small bracts (p. 142, 145).

In both transitions, the former of which had been already fully understood by the Bravais brothers, the sizes and forms of the fully grown phyllomes in the polymerous whorls clearly indicated the course of the original spiral.

Below in § 14 we shall meet with a fine case in the early binding whorls in the *Stellatae*, being the transition from the stipulate large foliage leaves, first to the exstipulate smaller leaves, and finally to the wholly abortive but still fertile bracts. The striking form differences in two successive dimerous whorls are fully sufficient here to determine the course of the original spiral.

§ 3. Decussate and whorled binding.

The fact that shoots with dimerous whorls are called decussate[1]), and that only shoots with three or more members in the whorls usually are called whorled, may have led sometimes to the belief in an essential difference between decussation and the

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[1]) The term decussate is derived from the latin verb decussare, to cross, a verb which is connected to decussis, the latin term for the symbol X. This word in its turn is believed to be due to a contraction of decem asses, ten pence.

As a botanical term the word decussate is used for instance in Linnaei Phil. Botan. Ed. quarta by Sprengel 1809, p. 93: [Folia] Decussata cruciatim opposita; in the first edition of 1751 we only find: [folia] Opposita, cum caulina folia duo, per paria decussatim, e regione collocantur.

The distinction of plants with opposed leaves as a group is to be found already before Linné; it was enounced by Tioch (59) in 1742 and by

„whorled" condition.

Yet a real contrast is not present, and when HOFMEISTER extends the term decussate to all alternating whorls (28, p. 460), one might stand up for this unusual practice from this point of view.

Practically however dimerous whorls are not only especially frequent, they are moreover more stable than polymerous whorls, in which variations in number are much more common. Because of these conditions dimerous whorls are much more important, and they are surely the best known. Our observations and quotations accordingly for the greater part will have to deal with decussate plants.

§ 4. Radial ¹) and dorsiventral ¹) binding whorls.

Already in 1829 SCHIMPER distinguished (45, p. 86) between two forms of decussation, that of the *Caryophylleen* and *Gentianeen* and that of *Salix purpurea* and *Fraxinus*, the first leaves of successive pairs being arranged in a spiral in the former, in the latter in a zigzag.

In 1844 WICHURA remarked that the form of decussation seems to influence the general habit of the plant: "Zuvörderst scheint die Ordnung, nach welcher die ungleich starken Knospen übereinander gereiht sind, auf das Wachsthum der ganzen Pflanze von Einfluss zu seyn; denn es ist gewiss nicht zufällig, wenn

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DE SAUVAGES (44) in 1743. TIOCH distinguished between plants with feuilles alternes and those with feuilles opposées; DE SAUVAGES knew four categories of phyllotaxis, feuilles opposées deux à deux; feuilles verticillées, ou rangées trois à trois, quatre à quatre, par étages; feuilles alternes, ou rangées l'une plus haut, l'autre plus bas, alternativement, and finally feuilles éparses, ou rangées sans aucun ordre constant.

LINNÉ borrowed his phyllotactical knowledge from DE SAUVAGES, copying these four categories and their definitions. But as the whole topic was absolutely strange to him, he added four other categories, one yet worse than the other.

¹) The different terms in use in Biology to designate the forms of symmetry in living beings cannot be discussed here.

The term radial, though being in a certain sense more correctly used to indicate spherical symmetry, as it is taken from the radiation of light beams, will be used here, in conformity with the common biological practice, for that kind of symmetry in which one single heteropolar axis is present, the morphogenetic forces round the axis being all the same. Examples are afforded by most roots and stems and by actinomorphic flowers.

The term dorsiventral will be used for parts with a heteropolar axis with different morphogenetic forces on two opposed sides, as in many rhizomes and in zygomorphic flowers.

wir bei den unter I aufgezählten Pflanzen, deren starke und schwache Knospenpunkte den Stengel gleichmässig von vier Seiten umgeben, meistens einem aufrechten Wuchs begegnen, während eine verhältnissmässig bedeutende Zahl der Pflanzen mit gebrochenen Spiralen einen kriechenden niedergestreckten Stengel zeigt, an welchem die beiden Längsreihen der stärkeren Knospenpunkte — gleichsam das Gewicht, welches den Stengel zur Erde niederzog — nach unten zugekehrt sind" (66, p. 183).

The same relation was pointed out by **Hofmeister** (28, p. 590), the explanation being exactly reversed; the "broken spirals" are not the cause of the horizontal growth, but they are induced in the inclined shoot under the direct influence of gravity.

Most botanists since **Hofmeister** have adopted a similar view, though expressed in the more acceptable way, that there are two essentially distinct forms of decussation, a radial one in which the first leaves are distributed in a spiral, and a dorsiventral one in which the first leaves form a zigzag.

From our point of view this conception has to be changed in so far as in both forms the original phyllotaxis being spiral, the first leaves are always arranged in a spiral, namely in a binary parastichy. The difference between the two forms is, that in radial shoots the adaptation to decussation, if imperfect, leaves a number of morphological phenomena which are all arranged in binary parastichies, whereas in dorsiventral shoots the dorsal and the ventral side being the site of different morphogenetic forces, the organs at the two sides have different plastics. If the dorsiventral decussation, as usual, is diagonally placed, the similar organs of the dorsal side as well as those of the ventral side must be arranged in zigzag lines.

As the presence or absence of dorsiventrality factors therefore may essentially alter the distribution of the similar organs on the shoot, the treatment of radial and of dorsiventral binding whorls in the present paper will be given in separate chapters, chapters 2—4 dealing with radial, chapters 5—7 with dorsiventral whorls.

§ 5. Material.

Most observations described in the present paper having been made on plants grown in the Groningen University Botanic Gardens or in some cases from plants growing wild in the neighbourhood of Groningen, I feel much indebted to the Direction of 's Lands Plantentuin at Buitenzorg for having sent me with characteristic liberality a chest with dried, but not compressed, branches of a number of plant species, decribed formerly from these Gardens by RACIBORSKI (41). This material in most cases proved excellent: *Crossandra* and *Casuarina* have been treated from them in the present paper.

Finally Ir. A. W. KLOOS kindly showed me some localities where *Salix purpurea* grows wild, in the neighbourhood of Dordrecht.

CHAPTER 2. RADIAL BINDING WHORLS IN GENERAL.

In radial shoots the binding whorl formation may be, and often is, so perfectly complete, even during the first visible developmental stages, that the resulting whorls are absolutely regular to the eye. Several instances might be quoted; that of the radial *Labiatae* may do for the moment, where the whorls are as regular as may be expected from products of nature, and where irregularities at any rate are only distributed by chance.

The best proof for this statement is the fact that WYDLER in his extensive observations (76, p. 201—212 general treatment, 77, p. 33—55 treatment of genera) never came across any traces of the original spiral, "trotz allen Suchens" (76, p. 204). Yet the whorls of the *Labiatae* are binding whorls (51, p. 678).

In a large number of plants there are however more or less distinct traces of the original phyllotaxis spiral, and these traces will be dealt with in the following paragraphs.

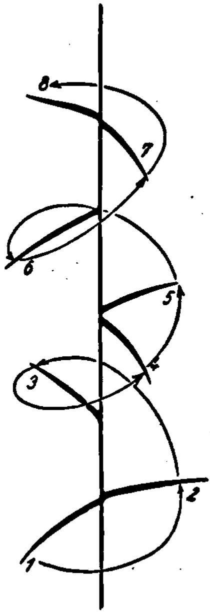

Fig. 7. *Apocynum venetum*, anomalous binding. From ZIMMERMANN (86, p. 273, fig. 4).

§ 6. **Irregular binding.**

Under the heading "Anomale Blattpaarungen" ZIMMERMANN deals with cases in which otherwise decussate shoots of *Apocynum venetum* display a local irregular binding order (86, p. 272).

As the most frequent case the condition is described, represented in fig. 7, copied from ZIMMERMANN, where in two successive dimerous whorls the second leaf of the lower whorl, 4, and the first leaf 5 of the higher whorl, are inserted at the same level, their partners 3 and 6 becoming in this way solitary odd leaves.

Yet the divergences are unchanged; those between 3 and 4 or between 5 and 6 remain 180°, and that between 4 and 5 90°. Exactly the same form of irregular binding was not met with in my material; as far as I see, it must be due to a normal dimerous binding in the youngest stages, with a due adaptation of the divergence angles to the decussation, but followed by a sticking together of two leaves in an abnormal way.

In the cases which came to my knowledge the conditions were less complicated. Fig. 8 gives a diagram of a particular shoot of *Centranthus ruber* in which the dotted lines indicate that two leaves are inserted at the same level.

After eight pairs of decussate leaves, a number of converging leaf pairs follow, amongst which one odd leaf, number 19, is intercalated. This seems to be the more general case, the original binding having skipped one of the primordia, without any further abnormal phenomenon.

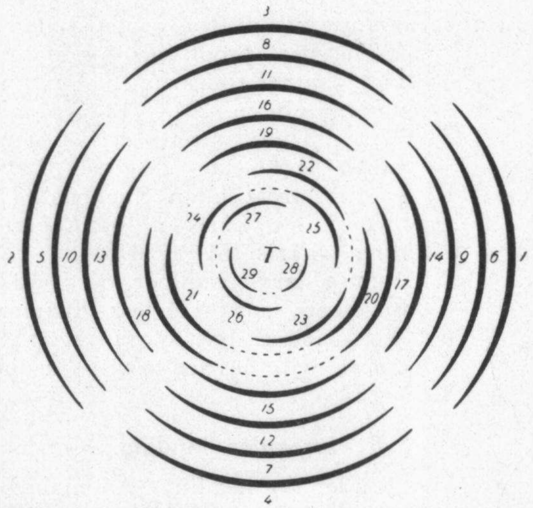

Fig. 8. ***Centranthus ruber*****. Diagram of particular shoot with convergences in higher leaf pairs; 19 an odd leaf, T terminal flower. Numbering of lower decussate leaf pairs derived from higher pairs.**

The occurrence of such an odd leaf in itself does not enable us to recognize any feature of the original spiral. But as soon as we have other means of determining that spiral (as in the present instance by the convergence of the leaf pairs), it is clear that the odd leaf must occupy a regular place in that spiral, and that its presence must change the positions of the higher leaf pairs completely. Thus it furnishes us with the means of checking the correctness of the determination.

The specimen of which fig. 8 gives a diagram was instructive in still another respect, as the stem at the node 19 sharply bent away from the leaf; this is what often occurs in decussate species at the insertion of a single leaf. DE VRIES pictures it for a shoot of *Dipsacus silvestris* with a dissolved leaf pair, two bends in the opposed sense being present at the two leaf insertions (63, pl. 7 fig. 2) and exactly the same was to be seen in a shoot of *Cajophora lateritia* of the Groningen Hortus with a dissolved leaf pair.

Evidently in some species with decussate leaves the growing leaf insertions develop strong displacing forces which are counterbalanced in the normal dimerous whorls, but cause a bend in the stem at a node with one leaf, and we may even say that in these species the opportunity is used for developing the leaves at an earlier stage than usual, so that for a time they are stronger than the apex.

This opportunity which exists in decussate plants, is not realized in stems with scattered leaves, for similar displacing forces are always to be observed where a podium bears a weak terminal and a strong lateral organ. This rule has been fully described by CELAKOVSKY under the name of the phytostatical law (13a).

In other decussate plants such an early developing of the leaves does not occur, so that in the case of dissolved pairs the stem remains straight; in § 33 such a case will be described for *Rhamnus Frangula*.

§ 7. The levelling of the organ insertions.

When we realize how easily longitudinal shifts in the plant are executed by slight variations of the longitudinal growth, it is no wonder that the slight longitudinal metatopies required for false whorl formation are quite perfect in most plants.

We might only expect to meet with a difficulty for the levelling in those plants where the leaf insertions are too large to permit a juxtaposition of all the leaves around the stem; in such cases the lower leaves have to remain inserted below the others.

In the late binding whorls of *Peperomia* we indeed found such a condition; whereas the longitudinal metatopies are perfect in di- and in trimerous whorls, the penta- and hexamerous whorls are different, the first leaves according to the original spiral being inserted lower than the others.

In early binding whorls however such cases do not seem to occur and this may be due to the circumstance that the binding takes place at a time when the leaf areas are still so small as to be levelled easily.

Imperfections in the levelling in early binding whorls, as far as I know, are only found in the dissolving whorls, to be dealt with in § 11, and moreover in abnormal cases.

Of the latter an instance may be quoted, described by CELAKOVSKY (13), being a specimen of *Vincetoxicum offinale* in which the second leaf of all dimerous whorls was inserted some mm above the first leaf; as the second leaf may be distinguished already by the fact that its bud is markedly stronger, these level differences undoubtedly corresponded to the original condition.

§ 8. The equalization of the angles between the whorl members.

The members of binding whorls having been induced at unequal horizontal distances, these distances have to be equalized when a perfect whorl is to be formed.

About the mechanism of the process we hardly know anything, we only know that it reaches different degrees of perfection in different plants and that it takes place at different developmental stages. Further we may suppose that the division of the available space between the growing whorl members will play a preponderant rôle in it. Indeed we often get the impression that the leaf bases in assuming equal sizes attain their equidistance by mutual crowding together. The free primordium in this process evidently is inactive, the leaf cushion and the leaf trace being responsible for the process.

In support of these views I might point out two instances, that of the late binding whorls in *Peperomia* and that of the early binding whorls in *Gypsophila*.

In *Peperomia*, for instance in *P. pulchella* (47) di- and trimerous whorls as far as can be judged by the eye have no horizontal metatopies at all; in the trimerous whorls we have therefore two large and one small angle. In tetramerous whorls of the same species the horizontal metatopy, though conspicuous, is not yet perfect, but in penta- and in hexamerous whorls the leaves are equidistant.

Yet in all these whorls the leaf insertions are so narrow that there is plenty of room between them; in pentamerous whorls the insertions are just about as broad as the spaces in between.

Evidently these leaves, though not contiguous, have sufficient mutual repelling forces in their inner parts within the stem to become equidistant, but in the di- and trimerous whorls the leaves have so much space as not to interfere with each other.

In *Gypsophila aculeata* all whorls are dimerous. In the whorls of the large foliage leaves the horizontal metatopy is perfect; when we pass upwards to the smaller, higher leaves and bracts the bulk relation between leaf and axis diminishes and the pairs, though perfectly levelled, are no longer opposed but their divergences are those of a normal system of the main series, as fig. 9 illustrates.

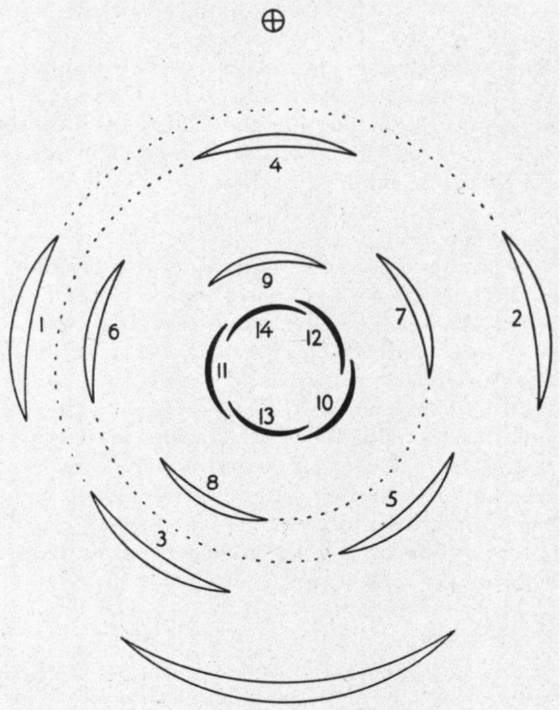

Fig. 9. *Gypsophila aculeata*, diagram of small inflorescence branch, with position of calyx of terminal flower. Dotted lines unite those bracts which are inserted at the same level.

Evidently here only the big leaves have sufficient mutual repelling forces.

Instances of decussate or whorled plants with imperfectly equalized angles between the whorl members may be found in large numbers in literature; some of these, pertaining to the adult condition of the whorls, will be reported first.

As early as 1831 AL. BRAUN described the fact that in *Silphium* the leaves in the higher pairs are approached together (4, p. 204) and in *Alsine media* he saw that the leaves converge on the side with the hair-line. As will be dealt with below this hair-line side really is the SW side, as might be expected.

A few years afterwards more extensive observations were published by the BRAVAIS brothers, who introduced the term "feuilles géminées" (9, p. 80) in the sense of dimerous whorls with converging leaves [1]). These geminate leaves are nothing but dimerous binding whorls without, or with imperfect horizontal metatopy.

The BRAVAIS' saw it in *Oxalis corniculata* where the small angle between the leaves was judged to be 137° 30', and the small angles in the successive pairs followed each other with a divergence of 85° (9, p. 80); they saw it further in *Alsine media* and *Lychnis chalcedonica* (10, p. 212); and moreover in the prophylls of many Dicotyledons of which they quote *Chrysanthemum Indicum, Fragaria* and *Ranunculus* (9, p. 81).

Similar facts are described by VON NÄGELI for *Galium Mollugo.* According to the author we can "an jedem Knoten eine stärkere und eine schwächere Hälfte unterscheiden, welche durch die beiden Blätter von einander geschieden werden." (37, p. 100).

The mutual relations of these convergences, and the course of the original spiral are absolutely indicated by the following sen-

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[1]) By many authors the term folia geminata, gepaarte Blätter, is used in quite another sense, namely for the two unequal leaves of many *Solanaceae,* which are due to a collocation of a sterile α-prophyll and a much larger β-prophyll of the next lower node, shifted by concrescence with its own axillary product. The BRAVAIS brothers call these latter pairs "feuilles rapprochées" (10, p. 301) and strictly distinguish between these very different cases.

Moreover they propose to call the trimerous and the polymerous whorls with unequal angles "feuilles tergéminées" and "multigéminées" (9, p. 84).

As the term geminate leaves for the *Solanaceae* is older, and is still in use in our time, it does not seem advisable to revive the use of the term in the sense of the BRAVAIS', the more as in the present state of our knowledge we can do quite well without any special term.

In still another sense the term is used by GOEBEL in his paper "Ueber 'gepaarte' Blattanlagen (24). Without quoting the BRAVAIS' or any other predecessor, GOEBEL designates any two organs as geminate when there is a fixed spatial relation between them, as for instance a petal and an opposed stamen, or a subtending leaf and an axillary bud.

It needs no remark that in any case the latter practice is to be avoided.

tence: "Die Ungleichhälftigkeit der Knoten schreitet mit der Spirale der Anfangsblätter regelmässig fort, und zwar so, dass die schwächere Hälfte dem Anfangsblatt vorausgeht, die stärkere demselben nachfolgt". (p. 101). A comparison with our fig. 10 shows that the smaller angle, ascending in an antidromous ¼ spiral like the homologous buds, precedes the second leaves of the pairs and follows the first leaves. What is called Anfangsblatt by VON NÄGELI therefore has to be the second leaf; we shall see later on that other facts lead to the same conclusion.

VON NÄGELI adds: "Ist die Zahl der blattartigen Organe eines Quirls ungerade, so befindet sich die grössere Zahl der Nebenblätter auf der stärkern Hälfte". This remarkable fact which I can fully confirm, proves that the number of stipules has a tendency to be greater on the LW-side, in connection with the available space.

The only fact reported by VON NÄGELI which is absolutely contrary to our views is that in *Galium Mollugo* the youngest leaves are exactly opposed, and only later develop a convergence by unequal growth of the node halves. Below, in § 13, it will be explained how VON NÄGELI by his observations could come to this, in all probability erroneous, opinion.

In a certain sense a still more important contribution to our knowledge was given by WICHURA in his excellent paper of 1844, a paper to which not nearly so much attention has been paid as it deserves. WICHURA finds that a terminal flower following on decussate leaves in some families shifts to a determined side; in the *Stellatae* and *Asclepiadeae* it shifts towards the side where, in the highest leaf whorl but one, the strong bud is formed, whereas in the *Sclerantheae, Alsineae* and *Sileneae* it is to the side of the weak bud in the same whorl. (66, p. 194).

As an illustration of this curious statement and to make clear why and how it may be relevant to our topic, fig. 10 may serve, in which four dimerous binding whorls and the calyx of a terminal flower are represented. The original places of the leaves 1—8 being indicated by crosses and their final positions by short arcs 1'—8', we see that the flower is not formed right between 7 and 8, but more at the side of 6'.

From this relation a shift in the direction of 6' may follow if, as is quite natural, the vegetative cone in initiating the formation of a terminal flower begins with a reduction of its area. The equilibrium between the expansion forces of the surrounding leaves with their buds on the one hand and the central area on the other, at that moment will be disturbed, and the

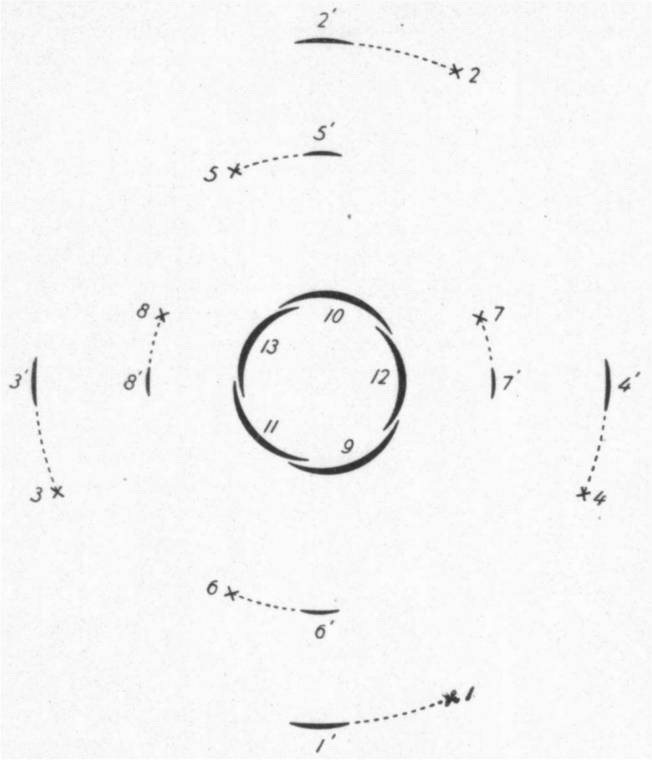

Fig. 10. Schematic representation of shoot with four dimerous binding whorls and a terminal flower with pentamerous calyx; 1—8 original places of leaf centres, 1'—8' actual leaf insertions.

expansions of the leaves 7 and 8 with their strong buds may quite well act together in driving out the terminal meristem from its central position (cf. 53).

Now as we shall see further on, in the *Stellatae* and in the *Asclepiadaceae* the second leaf of any pair subtends the strong bud; a terminal flower tending towards the side of leaf 6 will therefore be shifted towards that strong bud. In the *Caryophyllaceae* on the other hand it is the first leaf which has the strong bud; a shift towards leaf 6 there means a shift towards the weak bud.

WICHURA supposed that this shift of the terminal flower would be due to a mutual attraction of the polarized buds of the highest leaf pair. It will be clear however that it must be due to the imperfect horizontal metatopy of the originally spiral leaves and their buds at the critical developmental stage.

This interesting and important relation never seems to have been realized by any botanist, but for the **Bravais** brothers who already before **Wichura** had observed the same shift in some cases. Thus for instance in the *Caryophyllaceae,* about which they wrote that in the dichasium members the prophylls are "geminées" (10, p. 211), and they continue: "la preuve que, des deux divergences complémentaires, l'extérieure est la plus grande, est donnée par le pédicelle de la fleur terminale qui se déjette du côté de la feuille-mère".

Like so many other results of these eminent authors this keen insight into the elaboration of the plant form has escaped the notice of later botanists.

In this particular case there may be an excuse for this lack of attention, as the **Bravais'** in their paper complicated the whole topic by the assumption of a second cause for the shifts of the terminal flower, this time in the opposite direction. This second cause is what they call the excentricity (10, p. 294, 318) of the spurious axis [1]).

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[1]) Here it is not the place to discuss at length the influence of such an excentricity on the position of a terminal flower. But it may be worth while to explain what the authors understand by excentricity and why they attribute a shifting influence to it.

When in the double cincinnus of fig. 11 a spurious axis is formed on both

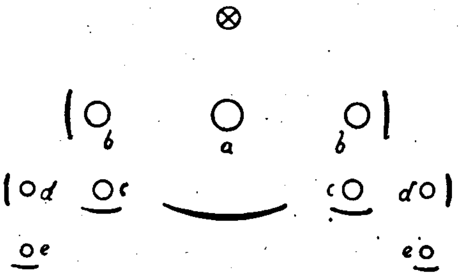

Fig. 11. Diagram of double cincinnus.

sides of the main flower *a*, this may result in the basal part of the main peduncle growing stronger on the abaxial side, so as to get an excentrical development, and this may tend to shift the unaffected upper part, the flower stalk proper of the main flower, to the adaxial side.

The possibility of such an effect not to be denied, we are by no means

In any case we may conclude that deficiencies of the horizontal metatopies in adult binding whorls are to be found in several plants, either by direct observation as done by the BRAVAIS brothers and by VON NÄGELI, or by indirect observation from the shift of the terminal flower, as carried out by WICHURA.

This having been stated, the same deficiencies must be expected even more so in the same plants during the developmental stages, and it is even not improbable that they may also be present in the youngest leaves of some plants in which the adult leaves are opposed, the convergences having disappeared during development.

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sure that the development of the flowers *c* would influence the condition in flower *a*, which is lower by two degrees. And especially we may doubt whether this excentricity would have the effect of shifting a terminal flower to the SW side, as the BRAVAIS' suppose to be possible.

As proof of the existence of such shifts by excentricity the authors quote three instances, those of *Symphytum*, *Anchusa* and *Centranthus* in which the main flower of a lateral inflorescence is shifted towards the adaxial side (10, p. 318, 319).

This fact itself is not subject to any doubt; what should have been proved however is that the adaxial side is the SW side as the BRAVAIS' tacitly assume.

For *Symphytum* and *Anchusa* we may be sure that the authors were mistaken this time; the adaxial side of the main flower of a double cincinnus is the LW side in these species, and the shift towards that side is accounted for by the convergence of the prophylls.

This follows from two statements made by WYDLER, who wrote about *Symphytum* (74, p. 679): "Mittelblüthe der Doppelwickel oft vornumläufig" which indicates in his terminology that the prophylls turn their LW side to the main axis, and about *Anchusa* (83, p. 365): "WRETSCHKO behauptet gegen meine Angaben, die Mittelblüthen der Dichasien seien niemals vornumläufig. Ich finde sie, nach zahlreichen auf viele Jahre vertheilten Beobachtungen, immer vornumläufig".

The same has been stated independently by SCHUMANN (53a, p. 302) who termed it the inverse position of the terminal flower, and by CELAKOVSKY (13a, p. 347).

In *Centranthus*, according to WYDLER, the flowers are opisthodromous (71, p. 386), so that the shift of the terminal flower in this plant should be towards the SW side.

As however the polymerous and pappus-like calyx does not betray any phyllotaxis, and as the prophylls according to my own observation distinctly converge on the abaxial side, I cannot avoid the conclusion that WYDLER's statement for which no arguments are given, neither l.c. nor in an earlier place to which WYDLER refers (70, p. 251), this time cannot be accepted.

The following observation tends to strengthen this opinion. In several specimens of *Centranthus ruber* the foliage leaves in the upper part of the stem show regular convergences in the pairs, ascending after a binary parastichy. In some of these cases, where in contrast to the normal condirather succinct, on the whole the expectation is realized.

Though the number of observations published in literature is rather succinct, on the whole the expectation is realized.

VON NÄGELI writes that the youngest leaves converge in: *Apocynum hypericifolium* (37, p. 96), *Alsine laricifolia, Spergula arvensis* (p. 97), *Galium rubioides* (p. 100), *Bignonia serratifolia* (p. 106), *Tagetes lucida* (p. 113), all cases in which the adult leaves are converging too.

Moreover he finds the same condition in *Dianthus plumarius*, where the adult leaves are opposed, and MÜLLER reports the same (36, p. 286) for *D. plumarius* and for *D. barbatus.* To these statements I may add that in *Blumenbachia Hieronymi* where the adult leaves also are opposed, the young leaves clearly are convergent, and that by tracing back the spiral which is determined in this way to the adult leaves, we always find that the second leaf of any pair subtends the flower.

In the quoted cases the observations are nearly always incomplete in that the correspondence between the convergences

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tion a terminal flower was developed, this flower was shifted to the LW side of the highest leaf pair, see fig. 12.

In these cases the highest whorl and the terminal flower had in every respect the same outward aspect as the parts in a dichasium. So it is the more probable that in the dichasia the shift will also be to the LW side of the prophyll whorl.

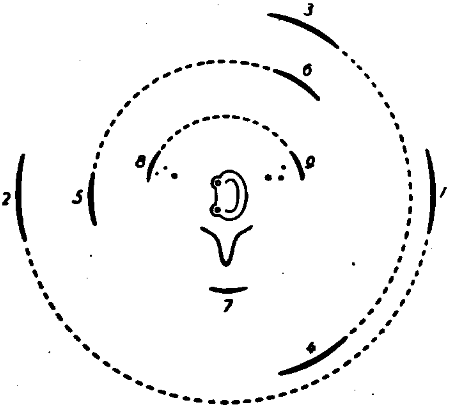

Fig. 12. *Centranthus ruber,* upper part of inflorescence with convergence of leaves in the higher pairs, one odd leaf (7), cincinni in the axils of 8 and 9, and a terminal flower. Dotted lines unite those bracts which are inserted at the same level. In the terminal flower the position of the spur and of the ovary has been indicated.

in the successive whorls has not been stated; this is due to the fact that in developmental researches it is hardly ever possible to observe more than a very few organs at the same time, in contrast with observations in the adult state, where usually long series of organs are available for examination.

The only favourable exception in the present case is that of *Anagallis arvensis,* about which von Nägeli writes (p. 109): "In der Terminalknospe stehen die Blattanlagen oft genau spiralig", a statement which pertains more to the later than to the first developmental stages.

Von Nägeli describes moreover a large number of plants in which already the first visible stages of the primordia are perfectly whorled. These are: *Fraxinus excelsior,* p. 95, *Vinca minor, Phlox* sp., *Calluna vulgaris, Hypericum quadrangulum, Androsaemum officinale,* p. 96, *Evonymus europaeus,* p. 97, *Galium Mollugo,* p. 100, *Antirrhinum majus,* p. 105, *Tecoma radicans* (ziemlich genau), p. 107, *Stachys angustifolia,* p. 108, *Clematis Viticella, C. Vitalba,* p. 110, *Lonicera* sp. (ziemlich diametral-gegenüber), *Acer Pseudoplatanus,* p. 112, *Humulus Lupulus,* p. 114, *Centranthus ruber, Aesculus macrostachya, Euphorbia Lathyris,* p. 115, *Sambucus nigra* (ziemlich regelmässig), p. 117, *Pisonia hirtella* (ziemlich regelmässig), p. 119.

According to our opinion, in these cases the metatopies must have taken place so early that they are already completed at the moment when the first primordia become visible.

As I am fully aware of the fact that most ontogenetists who only believe in the facts as observed under the simplex or rather under the microscope, will reject such a conclusion as a mere speculation, it is the more important that, though it may sound at first paradoxical, there are hard facts proving the real existence of the postulated shifts during the invisible developmental stages; these facts are found in the course of the leaf traces in the stem.

The induction of a leaf trace, especially that of its median bundle, taking place very early during the ontogeny, it may at least partly, very well occur in those stages preceding the bulging out of the leaf primordium. If it occurs before the completion of a horizontal shift, the consequence will be that when this shift occurs or when it is completed, only the upper part of the leaf trace will shift together with the leaf base, the lower part of the trace, since it is running downward in stem regions in the range of other phyllomes, remaining at its place.

For dimerous whorls this means that the two leaf traces when followed downward will bend out to the same side of the stem, namely to the SW side of the whorl to which they belong.

This indeed is what von Nägeli describes accurately for a number of decussate species as "symmetrisch-convergirendes Ausbiegen" of the traces; his descriptions are given without any comment and evidently without an understanding of the meaning of the phenomenon.

Accordingly the author only observes a few specimens in most species and does not mention any facts from which the course of the original spiral can be determined; thus for instance in *Vinca minor* and *V. major*, p. 96, *Evonymus europaeus*, p. 97, *Galium Mollugo* p. 101, *Ruellia maculata*, p. 106, *Clematis Viticella, C. Vitalba*, p. 110, *Tagetes signata* (gewöhnlich), p. 114, *Aesculus macrostachya*, p. 115, *Euphorbia Lathyris*, p. 116.

It is only for *Antirrhinum majus*, p. 105, that von Nägeli goes into detail; he writes that the median traces of the leaves of one orthostichy alternately bend to the right and to the left, and he gives a diagram of the vascular system of a seedling in horizontal projection, the higher internodes being drawn smaller (pl. 13, fig. 1).

This diagram has been reproduced in fig. 13 in a simplified form, all lateral traces being omitted and the median traces being numbered according to the original spiral. As we see, all traces, those of the cotyledons and the plumular leaves excepted, bend to the right when their number is odd, to the left when it is

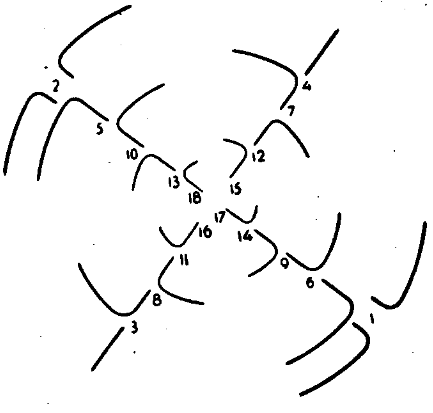

Fig. 13. *Antirrhinum majus*. Median traces of leaves of seedling plant in horizontal projection. Simplified, from Nägeli (37, pl. 13, fig. 1).

even [1]).

A shift of all leaves in the direction of the lower part of their traces would change the whole decussation into a regular pattern of the main series. We are therefore justified in saying that in this plant where the primordia from the beginning are decussate, the leaf areas must have stood in a spiral system.

In all probability the same result may be reached in the other quoted species with symmetrically converging leaf-traces, when submitted to a special investigation.

§ 9. The adaptation to alternation.

In many plants binding whorls are accurately alternate, at least as far as can be judged by the eye. As it is not to be expected that the original spiral in such cases will always have had the exact divergence for the realization of alternation, we may suppose that in these plants an adaptation to alternation takes place, for which only a stem torsion may be responsible.

In other plants the alternation is not attained, and by the difference from the alternating condition we may glean some idea of the original divergence. In the present paragraph only decussate plants will be dealt with.

For decussation, as set forth in the introduction, only a divergence of 135° leads, without any stem torsion, to a rectangular crossing of the leaf pairs. In all other cases the four orthostichies are transformed into winding spirals, running against the original spiral for divergences under 135° and being homodromous to the original spiral for larger divergences.

As the systems of the main series usually have divergences between 135° and 144°, we may expect that deviations from rectangular crossing will usually be due to an excess of the divergence.

In literature a number of observations on skew crossing has been recorded by various authors. In many cases their records are insufficient for our purpose, what we want to know being especially the angular value of the "prosenthesis", the divergence between the last leaf in a whorl and the first leaf of the next higher whorl, or the angle between cyclure and cyclarch.

Thus Al. Braun mentions that the leaf pairs are arranged spirally, not rectangularly in: *Silene Zawadskii, Coronaria flos cuculi, Viscaria purpurea, V. alpina, Sagina nodosa, Spergularia rubra, Spergula arvensis* (6, p. 387).

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[1] In the preliminary communication (48) where the same figure was given, the words right and left have been in mistake interchanged in the text (p. 232).

In other cases the indications are more complete, and then we may calculate the original divergence, unless a stem torsion may have taken place, in which case the original divergence may have been still more remote from 135°.

Species in which the divergence must have been less than 135°, and consequently the prosenthesis less than 90°, are not on record. There are some statements by Rohrbach (42, p. 299) which if they were correct, would pertain to such cases, but in all probability they are erroneous. They are: *Arenaria dicranioides*, prosenthesis $\frac{1-{}^{2}/_{3}}{2}$; some unnamed *Sileneae*, prosenthesis $\frac{1-{}^{3}/_{4}}{2}$, and *Thylacospermum*, prosenthesis $\frac{1-{}^{5}/_{6}}{2}$. These values, amounting to 60°, 45° and 30°, would imply divergences of 120°, 112.5° and 105°. As these divergences would fall outside the realm of the main series they are extremely improbable, and as no evidence of any kind is given in favour of them, they may be discarded, the more as in another paper by Rohrbach, issued a year later (43) they are omitted.

Turning to species with divergences of more than 135°, most records are of species with 144°. This may be due to the fact that in such cases the sixth leaf pair lies above the first, the fifth lying above the first in normal decussation. So when the observations are made by trying to determine the first pair lying above a given pair, all intermediate cases between 135° and 144° must give rise to more complicated formulae.

The only instances of intermediate cases known to me in literature have been given by Al. Braun (in 43, p. 18) for *Lychnis chalcedonica*, as prosenthesis $\frac{1+{}^{4}/_{9}}{2}$ and $\frac{1+{}^{3}/_{7}}{2}$. These values being along SW 100° and $102^{6}/_{7}$°, correspond to divergences of 140° and $141^{3}/_{7}$°.

Observations pointing out a divergence of 144° are given by Al. Braun for *Globulea obvallata* (4, p. 378) for which he denotes a phyllotaxis of ($\frac{1}{2}$) ${}^{3}/_{10}$, i.e. $\frac{1}{2}$ or 180° in the pairs and 108° as prosenthesis; by Rohrbach (43, p. 18) for *Silene acaulis* and *S. viscosa*, for which he mentions a prosenthesis of $\frac{1+{}^{2}/_{5}}{2}$ or 108°; further, though in a less clear form, by Wydler for *Sagina procumbens* for which he gives (73, p. 326) the same unexplained formula as two pages earlier for *Silene acaulis*, namely $\frac{1+{}^{3}/_{5}}{2}$. Evidently he does not give it as representing a prosenthesis, as in the numerous cases in which he determines a prosenthesis this is always mentioned instantly. Moreover as a prosenthesis the formula would be erroneous. Perhaps it means a sequence of two divergences of 180° and 108°, and then it amounts to the same thing stated by ROHRBACH. Moreover he writes about *Cherleria sedioides* (73, p. 328): "die Paare bald rechtwinkelig und häufiger spitzwinkelig, so zwar, dass je die fünften Paare über einander fallen." This no doubt is the same relation.

My own observations on *Arenaria balearica* taught me that the obliquely crossing pairs form four steep parastichies, the sixth pair lying above the first; the strong buds form an antidromous spiral with 72° divergence. So the prosenthesis is 108° and the divergence 144°.

Decussate species in which the original divergence must have been more than 144° seem to be rare. The only records known to me are those by AL. BRAUN for *Mercurialis perennis* and *Acer platanoides* (4, p. 377); the leaves in the former and the bracts in the inflorescence of the latter are described as having a phyllotaxis of $(\frac{1}{2})\ {}^{2}/_{6}$. From this formula it follows that the prosenthesis is 120° and the mean divergence 150°.

As we shall see in our § 18 and 20 in both species the mean divergence is really rather high; according to my observations something like 145°. But there were no indications in my material to justify the assumption of a divergence of 150°.

§ 10. The elimination of the differences in age of the whorl members.

1. Leaves.

Perhaps the most remarkable adaptation is the fact that in early binding whorls the members, even though decidedly spiral in origin and induced at different times, yet appear at the same time as primordia, and then are of the same size. Especially when we consider the relatively small biological advantages the plant may get from this adaptation, we cannot but admire its perfection.

The way in which the adaptation works must be that the whorl formation occurring very early, before the bulging out of the first primordium, the special growth of the older leaves is postponed until the younger leaves are in the same condition, so that a simultaneous and equal growth is possible from the moment of bulging out.

In *Peperomia* with its late binding nothing of this kind is to be observed; the leaves arise at such a time and have such sizes as correspond to their order in the spiral arrangement, and the differences remain visible until the adult state is reached. A similar condition is to be observed in *Anagallis coerulea.*

In early binding whorls on the other hand the elimination of the differences in age is nearly, or even wholly, perfect. Quite a perfect equalization is present for instance in *Viscum album* and in *Fraxinus excelsior* (MÜLLER 36, p. 280); obvious differences in the time of bulging out of the primordia on the other hand remain in *Dianthus plumarius* and *D. barbatus* (MÜLLER ibid) and in *Silene* (ROHRBACH 43, p. 13).

In the *Stellatae* (in *Galium rubioides, G. Mollugo, G. purpureum, Rubia tinctorum*) VON NAEGELI observed differences in size between the two leaf primordia of a pair. However, as he did not know that the advanced bud is subtended by the second leaf, the bud sizes prevented him from realizing the actual conditions. He wrote: "In der Achsel der beiden Blätter treten schon sehr frühe Knospenanlagen auf; die des Anfangsblattes erscheint vor der andern, und hat in der Entwickelung auch immer einen Vorsprung. Ich bemerke übrigens, dass das Wachsthum der Blätter sehr oft ein umgekehrtes Verhältniss zeigt, indem das Anfangsblatt sich etwas langsamer ausbildet und daher kleiner ist" (37, p. 100). So notwithstanding his erroneous starting point VON NAEGELI correctly saw that the second leaf (his Anfangsblatt) is smaller than the first leaf, and at the same time gave a striking proof of his trustworthiness and accuracy as an observer.

In such cases in which the age differences of the leaves have been observed, it might have been determined whether the developmental order corresponds to the sequence in the spiral. The only author who ever seems to have investigated this question is ROHRBACH (43, p. 14). His exposition of the facts is far from clear however, and his figures are not convincing. Yet there is hardly any doubt that the expected correspondence really will exist.

2. Buds.

The leaves in the binding whorls being originally of different ages, their axillary buds of course may be in the same condition, the supposition that the buds are only induced after the leaves have been equalized in age not being very probable.

In many cases these differences are equalized too, and the resulting buds are all equal in the same whorl or at least their differences are small and not distributed in a regular way.

Such equal buds are present for instance in the following decussate plants: *Coffea arabica, C. liberica, Petunga Roxburghii, Sarcocephalus Junghunii, Garcinia cornea, G. echinocarpa, G. ferrea, G. Livistonii, G. Mangostana, G. Morella, G. Roxburghii, Gnetum Gnemon, Pisonia aculeata, Eupatorium* spp, *Bacharis* spp (all after RACIBORSKI 41, p. 19).

In many other plants the buds are more or less different, or as WICHURA called it, they are polarized (66). As soon as this is the case, the differences must be distributed according to a definite rule, due to the spiral origin; according to § 2 this order for decussation amounts to an arrangement in two homodromous spirals with ¼ divergence. Hence the familiar fact of the bud spirals which already in 1601 had attracted the attention of HONORIUS BELLUS who wrote about a plant named *Ossar* (according to IRMISCH 30, p. 50 = *Asclepias gigantea*): "Folia.... opposita...., ex quorum alis multi rami nunc erumpere incipiunt, non quidem ex omnibus, sed alternatim, ita ut, si a primo initium sumens, lineam ab uno ad alium ducas usque ad ultimum, perfectissime lineam helicen describas".

This "polarization" may assume the following three forms: the buds may have the same plastics and only differ in size, that from the first leaf being furthered; they may have the same plastics, but that of the second leaf may be advanced, and finally the buds may differ in plastics.

The occurrence of these three forms which is unparalleled in their subtending leaves requires some explanation.

It proves that the differentiation of the buds is influenced in some way by the whorl formation: evidently the buds of different age react differently to the simultaneous action of the whorl forming factors. In the case where the bud of the first leaf is furthered, this is not simply due to the fact that this bud is the first to attract the available nutritive substances for its development; we may safely infer that it is the developmental stage of the bud, being different from those of other buds, which makes it behave differently.

Thus in this way specializations are reached in the buds, which in the subtending leaves are only paralleled by those developed under the influence of dorsiventrality factors.

a. The bud from the first leaf is furthered.

This reaction is proper to the leafy shoots in the *Sileneae, Alsineae, Sclerantheae* (WICHURA 66, p. 194), *Gentiana* (SCHIMPER 45, p. 86) and *Helianthemum* (WYDLER 68, col. 213).

Moreover it may obtain in the prophyll whorls of many inflorescences, where it is known as the furthering from *a*. So in many *Ranunculaceae, Tribulus, Erythraea, Asclepiadaceae, Apocynaceae,* as may be read in Eichler (20).

The difference between the buds may be in any grade of importance.

In some specimens of *Stellaria aquatica* a reversal of the bud spiral has been described by Matzke (35, p. 492), "at least apparently". The described specimens are four branches out of more than 300.

According to our views such a reversal can never be real, and conversely if it really existed our views would have to be changed. A reversal however may arise apparently by the abnormal development of one or two buds.

Indeed as soon as a strong bud through some accident stops its growth, so that the opposed bud can overtake it, this simple fact simulates the existence of two successive reversals. Now we may be sure that the start the strong bud has of its weak neighbour is only due to influences acting during the very early developmental stages and that there may often be circumstances through which the weak bud later gets ahead.

Accordingly Matzke's specimens do not show a real and lasting reversal, but they are such as may be due to one or two "faults" of this kind in the development[1]).

b. The bud from the second leaf is furthered.

This is to be observed in the vegetative region of the *Stellatae* (Wichura 66, p. 194) and in the vegetative region and the sympodial branching of *Asclepias* and *Vincetoxicum* (Schoute 53).

In inflorescences it is known as the furthering from β, which is a common condition in Dicotyledons.

Furthering of a bud may sometimes bring with it the development of an accessory bud. In *Galium saccharatum* the Bravais brothers found (10, p. 346) that only one of the two buds of any node was accompanied by an accessory bud, these buds ascending in a $\frac{1}{4}$ spiral. No doubt these will have been the buds from the second leaf.

Franke sometimes observed a "reversal" of the bud spiral in some *Stellatae*. These reversals may have been of the same kind as those in *Stellaria* described by Matzke. A detailed description is not given.

c. The buds differ in plastics.

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[1]) Plant 15 one fault, in node 2; plant 4, branch 4 one fault in node 5; plant 11, branch 2 two faults, in node 2 and 4; plant 18, unnamed branch, two faults in nodes 5 and 6.

This occurs for instance in *Borreria ocymoides,* a *Rubiacea* (Raciborski 41, p. 38), where one of the two leaves subtends a vegetative shoot, the other an inflorescence, both ascending in a ¼ spiral. A similar case will be described below in *Blumenbachia.*

Wichura writes (66, p. 185) that "polarized" buds may be equidistant or may converge in a regular way, "indifferent" buds always being equidistant.

This rule, though no doubt subject to many exceptions, may be the expression of the fact that a lack of differentiation between the buds is more likely to occur in perfect whorl formation, whereas specialization of the buds may be expected rather in plants where the differences in age and the original spiral positions of the organs may still be recognized.

One of the most remarkable features of this "polarization" of the buds is the fact that with the transition to another region of the plant the branching method often changes entirely, as appears from the following instances.

a. In the vegetative region the bud from the first leaf is furthered, in the floral region the flower from β is furthered: *Caryophyllaceae* (§ 13), *Cajophora* (§ 17).

b. Exactly the reserve, in the vegetative region furthering from the second leaf, in the floral region from α: *Stellatae* (§ 14).

c. In the subterranean scale-bearing stem furthering from the first, in the leafy overground axis from the second leaf: *Gentiana Pneumonanthe* (§ 16).

d. A more complex case is afforded by *Asclepias* and *Vincetoxicum;* in the vegetative region: buds from the second leaf furthered; in the general inflorescence: the sympodium members from β, according to the same rule therefore; in the sympodium members: scattered, not decussate bracts, all being fertile; in the partial inflorescences: flowers furthered from α (53).

In other cases the rules are less pronounced:

e. In the vegetative region: a weakly expressed advancement of the buds from the second leaf, in the floral region: furthering from β: *Erythraea* (§ 16).

f. No rule of furthering in the vegetative region; in the floral region furthering from α: *Vinca* (§ 15).

These facts really seem to point out that the two buds which are equalized to a certain degree, but not wholly, and which in any case have been subject to a different pre-treatment, react differently to the action of the morphogenetic forces, which are the same throughout the dimerous whorl.

When in another region of the shoot other morphogenetic forces become active, it is no wonder that the reaction may change too, and that even the furthering may be inverted.

We might even suppose that a bud during a certain stage of its development is specially adapted for a certain line of morphological differentiation.

If for instance we imagine that a younger bud is more easily converted into a flower and an older one more easily into a vegetative bud, we might expect a method of branching such as prevails in the *Caryophyllaceae.* For in such a case in the vegetative region where the flower forming factors are weak or wanting, the buds from the first leaves, as being older, will grow out into vegetative buds; in the floral region on the other hand where the flower forming factors prevail, the younger buds from the β-prophylls will develop into flowers.

§ 11. Discontinued whorls.

A shoot in which the binding factors are active may form its whorls as long as its growth lasts. This is for instance the usual condition in diplo- or pleiocaulescent species, where the first axis only forms foliage leaves, as in the *Labiatae.*

In many other species and especially in haplocaulescent plants the whorls sooner or later may disappear. In a great number of cases this occurs when the floral region is reached; for instances see SCHOUTE (51, p. 678). As WYDLER puts it (69, p. 736): "der Uebergang.... zeigt sich am häufigsten da, wo die Inflorescenzen auftreten, gleichsam als hätte die Nachbarschaft der Blüthen einigen Einfluss auf die Zerstreuung früher zusammenhaltender Blattpaare".

The transition between the whorled and the spiral region may be quite sharp, all of a sudden. In many cases however it is gradual, almost insensible, and this kind of transition has been very aptly called solution (Auflösung) by WYDLER. Previous authors used to call it dissocation (SCHIMPER 45, p. 85, 88: Auseinanderrücken; BRAUN 4, p. 346, 349: Zerstreuung, DUTROCHET 18: dissociation); the terms solution and dissolving whorls will be used here.

If this discontinuation of whorls is really due to an inactivation of the binding factors, we may expect that the phenomena to be observed in these shoots will throw light on the normal action of these factors; in discussing these phenomena we shall have to deal separately with the gradually and the suddenly discontinued whorls.

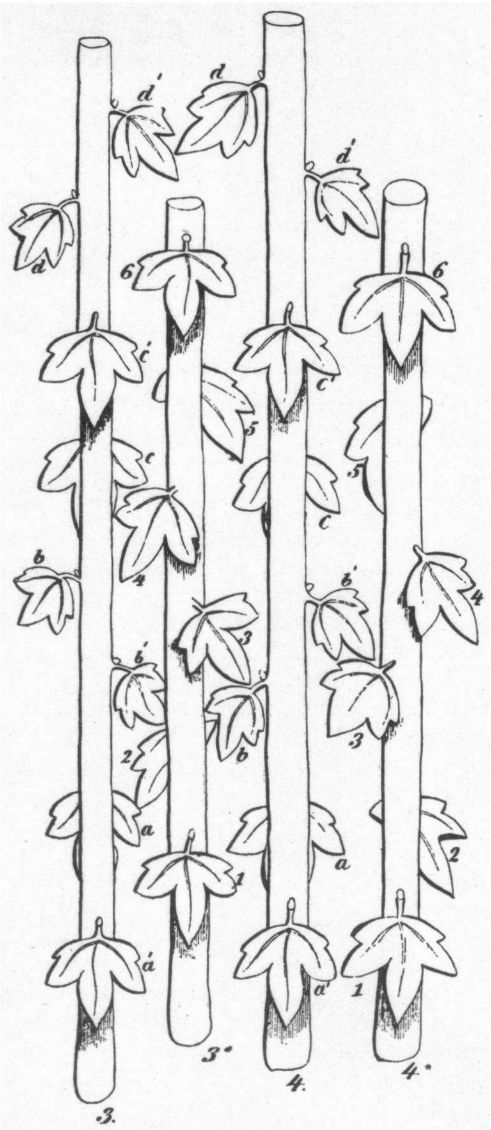

Fig. 14. *Acer campestre,* two branches with dissolving whorls, from DUTROCHET (18, pl. 8). 3 and 3* basal and upper end of branch with transition to a left-hand spiral phyllotaxis, 4 and 4* same to right-hand spiral.

1. Dissolving whorls.

The first author to describe dissolving whorls was Dutrochet, who observed the transitions between whorled and spiral regions in the shoots of *Fraxinus excelsior* and *Acer campestre* (18, p. 214). According to him the transition commences by a longitudinal dissociation of the pairs, in such a way that in any two superposed pairs the difference in level is reversed; in support of his description Dutrochet adds two figures 3 and 4, reproduced here as fig. 14.

In higher regions of the same shoots the leaves moreover are subject to lateral shifts in such a direction that a $^2/_5$ arrangement ensues (fig. 14, 3* and 4*).

For our purpose the important feature in this description is that at first only one kind of metatopies, those in the longitudinal direction, slackens, whereas the relaxation of the transverse metatopies follows later. If the transition from decussation to spiral arrangement was only the outcome of the formation of new organs in the largest available spaces, these two kinds of shift should be absolutely correlated.

Analogous facts of the disappearance of the separate processes of binding whorl formation at different levels are met with in numerous other species.

In the papers by Wydler we find a great number of observations on the region where usually the transition from decussation to spiral phyllotaxis takes place in a species, and in many cases the author adds the statement that the rectangular crossing remains unimpaired in the same whorls where the insertion levels are clearly different. The latter in most cases, with a more or less perfect accuracy, follow the rule of the decussation of the *Caryophyllaceae,* i.e. the level differences in superposed pairs are reversed.

These conditions are mentioned by Wydler for the following plants: *Epilobium parviflorum* (am öftersten.... mit vielen Störungen, 74, p. 221); *E. montanum* (in part of the shoots, ibid. p. 222); *Portulacca oleracea* (ibid. p. 364); *Eupatorium cannabinum* (in part of the shoots, ibid. p. 501); *Phlox paniculata* (Mitt Beginn der Inflorescenz löst sich die paarige Blattstellung auf, entweder mit Beibehaltung der rechtwinkligen Stellung oder mit Uebergang in die Spiralstellung, ibid. p. 658); *Scrophularia* (in der Region der Blüthenzweige lösen sich die Paare auf, ihre rechtwinkliche Stellung noch beibehaltend 76, p. 137); *Veronica serpyllifolia* (In der Blüthenregion lösen sich die Blattpaare auf, Anfangs mit Beibehaltung der decuss. Stellung, wo ich dann ihre Aufeinanderfolge derj. der Spross- und Blattstellung der Caryophylleen entsprechend finde, ibid. p. 191); *Verbena officinalis* (Mit d. Auftreten der Hochblätter löst sich die paarige Stellung auf, Anfangs noch mit Beibehaltung der rechtwinklig decussirten, dann in Spiralstellung übergehend, welche durch d. Inflor. hindurch vorherrscht, 77, p. 56); *Salsola Kali* (ibid. p. 135); *Chenopodium hybridum* (main axis with 2—6 usually dissolved rectangular leaf pairs, ibid. p. 137); *Ch. urbicum* (main axis, usually, id. p. 139); *Ch. murale* (id.); *Ch. album* (id. p. 140); *Ch. polyspermum* (id. p. 142); *Ch. glaucum* (id. p. 143); *Atriplex patula* and *A. latifolia* (id. p. 144); *Euphorbia helioscopia* (in most cases, 79, p. 10).

A few observations of my own may follow.

In *Helianthus annuus* (§ 24) and in *Epilobium hirsutum* the transitions occur in three ways: the first level difference and the first convergence are either present in the same leaf pair, or the level differences or the convergences arise first, the other phenomenon only occurring one or more nodes higher.

In *Erythraea Centaurium* no level differences were observed, but in the highest leaf pairs, in contrast to the condition in the lower and the middle stem region, convergences are invariably present, ascending in a ¼ spiral; usually in three, sometimes in two leaf pairs.

In *Gentiana Pneumonanthe* the conditions are similar; no level differences, but convergences in the higher leaf pairs at the SW side. The observation is facilitated by the fact that the two leaf cushions on the stem are separated by grooves which are clearly narrower in the case of a convergence at the SW side.

In *Dahlia variabilis* and in *Cosmos sulphureus* I only observed cases in which the first level difference and the first convergence occurred at the same node.

2. Suddenly discontinued whorls.

Whereas in dissolving whorls the identity of the spiral, being hidden in the decussate part and obvious in the spiral part, may be read directly from any specimen and consequently needs no special proof, in suddenly discontinued whorls, such as may occur in the calyces of terminal flowers or sometimes in bracts (*Asclepias*), the proof cannot always be given.

It however becomes possible as soon as the original spiral may be determined in the decussation, by means of a bud spiral or any other phenomenon; so we may say that a calyx spiral must always be (and is) antidromous to the bud spiral under it; moreover the position of sepal 1 is governed by strict rules.

In a pentamerous flower sep. 1 according to WYDLER nearly always falls at an angular distance of 126° from the second leaf of the highest pair (73, p. 315); it is only in some exceptional specimens that the distance may be 90° (*Dianthus barbatus* 73, p. 317, *Cerastium arvense, Dianthus Caryophyllus, Gypsophila repens, Lychnis Flos-cuculi, L. chalcedonica* (83, p. 319).

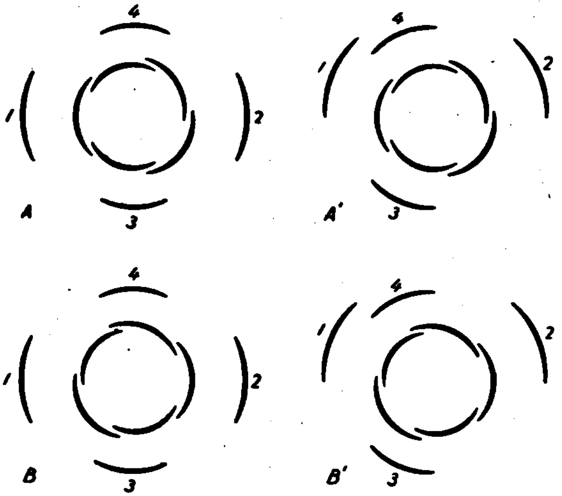

Fig. 15. Mode of junction of pentamerous calyx to dimerous binding whorls; A most frequent form; A' same, without horizontal metatopies of leaves; B and B' analogous representation of less frequent form.

Our fig. 15 will make clear that in both cases the spiral is continued in the same sense; 15A corresponds to WYDLER's figure 1 (73, pl. 6). The difference between the two modes of junction 15A and 15B is evidently due to a different way of adaptation of the pentamerous calyx whorl to a regular junction with the dimerous whorls; in 15A' and 15B' where the horizontal metatopies in the binding whorls (not in the calyx) are supposed to have been left out, the angular distances between leaf 4 and sepal 1 amount to 148½° and to 112½°. ¹)

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¹) The condition represented in 15 A had already been observed correctly as early as 1846 by WICHURA (67, p. 231), but had been completely misunderstood. Having observed that in the main axes of the *Caryophyllaceae* the first sepal lies at a divergence of 54° from the highest strong bud (from the first leaf of the pair) and in the dichasium members at 126° from the strong bud (from β) which amounts to the same condition, he concluded that there was a reversal of the phyllotaxis and of the cladotaxis.

These observations are quite sufficient to prove that the higher spiral is nothing but the continuation of the spiral hidden in the whorled part, a fact which is essential to our purpose.

Yet in some exceptional cases there is still additional evidence to be got from the phenomena observed in incomplete whorls. In some species we may occasionally find a specimen in which between the highest normal whorl and the spiral part one single partial whorl is present, consisting in decussate plants of a single odd leaf.

Of course the position of such an odd leaf has to correspond with the course of the lower spiral in the decussate part, as well as with the spiral above it.

This indeed has been described by **Wydler** for the following cases: *Sedum stellatum* (74, p. 380); *Saxifraga oppositifolia* (ibid. p. 388); *Swertia perennis* (id. p. 643), all for main axes; *Vinca* for a sympodium member (id. p. 630).

In other cases **Wydler** only describes the correspondence with the lower spiral (*Gentiana nivalis,* ibid. p. 649; *G. Pneumonanthe, G. campestris,* id. p. 764) or with the higher spiral (*Androsaemum officinale* 73, p. 365; *Hypericinae* 82, p. 52); in still other cases he only mentions the occurrence of half whorls (*Gentiana cruciata, G. asclepiadea* 74, p. 646).

To these observations I may add that in *Gypsophila aculeata,* as shown in our fig. 9, the position of the odd leaf is exactly as it should be, and the same was observed in *Hypericum quadrangulum,* in *Dianthus plumarius* (involucre) and in *Centranthus ruber.*

In these cases in which an incomplete whorl is formed we may say that the number of leaves available for whorl formation was not a multiple of the whorl number. As this condition is a rare exception, we are led to the reverse question of how it is that nearly always the number of leaves does constitute such a multiple.

The only possible answer to this question seems to be that the whorl formation occurring early, the induction of a calyx or other spiral formation usually takes place immediately above the last induced whorl. And only in such cases where the calyx or other spiral formation is induced some distance above the last whorl, the number of intermediate leaves being indeterminate, may incomplete whorls be formed.

§ 12. Lateral connation in binding whorls.

Lateral connation of phyllomes, only being possible between leaves of about the same insertion level, is seldom found in spiral phyllotaxis where it may only occur when the stem does not elongate. In true whorls it is not to be expected either, as these are always intermixed with spiral patterns.

It is only in false whorls that lateral connation may freely occur. Accordingly many floral belts are more or less connate, and in foliage leaves the same may occur in binding whorls, *Equisetum* being a well-known instance.

If in plants with such false whorls the connation has once been incorporated into the leaf plastics, it remains of course in the case of biastrepsis (51, p. 673), and even in the case of inactivation or loss of the whorl forming factors.

The best instance of such a condition is probably offered by *Phyllactis rigida*, a *Valerianacea* described by Benoist (1, 2). In this species the leaves are usually connate in two parallel spirals (1, p. 490, 2, p. 370), as indicated in our fig. 16A, copied from Benoist. A leaf of any spiral lies above the space in the next lower coil of the other spiral, but not in the middle of it as any one leaf is nearer to the lower of the two leaves under it.

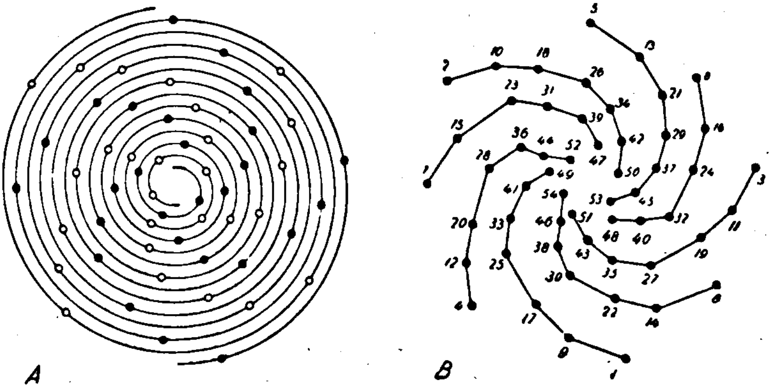

Fig. 16. *Phyllactis rigida*, A diagram of specimen with connation of leaf bases according to the two binary parastichies, from Benoist (2, p. 565); B same with numbering of leaves after their order in the spiral and with indication of the 8 parastichies.

Benoist takes this phyllotaxis as a modification of decussation, but when we number the leaves in their natural succession, as in fig. 16B, we see that it is a normal spiral pattern without any trace of decussation or of binding whorls in it. We cannot tell whether leaf 1 and 2 should form a pair, or 2 and 3, their distances being equal.

Yet the connation which is present in so many of the *Valerianaceae* with binding whorls, and which is quite in place there, has been preserved in this species, notwithstanding the loss of the binding factors; as the stem is quite condensed, there is no harm done.

This view is corroborated by the fact that as BENOIST describes, the connation does not always follow the binary parastichies, but that in some specimens it follows the genetic spiral, in others it unites the two edges of one single leaf, so that amplecting leaves are formed (2, p. 371).

CHAPTER 3. RADIAL BINDING WHORLS IN SOME SPECIAL PLANT GROUPS.

The binding whorls of different plant groups often being different in minor points, or complicated by secondary phenomena, the present chapter will deal with the peculiar forms of binding whorls in the plant groups named above.

In view of the frequency and importance of dimerous whorls decussation will be chiefly treated.

§ 13. Caryophyllaceae.

Not all *Caryophyllaceae* have whorled foliage leaves; a spiral phyllotaxis is met with in *Corrigiola* (78, p. 85), *Telephium* (74, p. 371), *Dysphania* (21, 3, 1b, 1889) and *Lyallia* (42, p. 298). Evidently no binding factors are present in these genera.

Neither are the *Caryophyllaceae* with binding whorls always radial; a zygomorphy of the vegetative region is present in *Paronychia, Herniaria* and some other genera.

Yet the great majority of the *Caryophyllaceae* has radial binding whorls, and these are nearly always dimerous; a species with trimerous whorls in the upper part of the shoots has been described by MATTFELD under the name *Pycnophyllum kobalanthum* (34).

The most important features of these decussate whorls having already been mentioned in the previous chapter, two particular features may be treated here, the hair ridge of *Stellaria media*, and the decussation of the involucre of *Dianthus*.

1. The hair-line of *Stellaria media.*

A well-known feature of *Stellaria media,* even used in the Floras as a diagnostic character, is the development of a one-sided longitudinal hair ridge on every stem internode. These hair-lines ascend on the successive internodes in a ¼ spiral, which is due to the fact that it extends from the strong bud of the lower node to the interfoliar space above it of the higher node.

The BRAVAIS brothers were the first to remark (10, p. 212) that the interfoliar spaces from which the hair-lines descend are the SW divergences, in the dichasium members as well as in the main stem, and they ask: "Quelle est la cause de cette série longitudinale? nous l'ignorons; sont-ce les cils des bords décurrens de deux pétioles voisins soudés latéralement?"

WICHURA, after mentioning that similar hair-lines are present in *Stellaria pubera, S. bulbosa, S. viscida, Cerastium sylvaticum,* and, though less developed, in *Saponaria calabrica, Cerastium collinum* and *C. triviale,* (66, p. 184) writes of the ridge: "Die physiologische Bedeutung desselben auseinander zu setzen, würde ausserhalb der Gränzen unserer Untersuchung liegen, und nur im Vorbeigehen sey es daher erwähnt, dass er zuverlässig mit der Ernährung des Knospenpunktes im nächsten Zusammenhange steht, aus dessen Axille er entspringt, oder richtiger, in dessen Axille er verläuft."

Translated into more modern terms we might say that we have here two suppositions about the morphogenetic forces for the hair-line, one being connected with the convergence of two leaves at the apical, the other with the development of a furthered bud at the basal end of the ridge. In support of his view WICHURA observes that in the lower internodes of *St. media* a second less dense hair-line is sometimes developed above the weak bud, which bud in these cases develops a small branch.

He should have added that for the first internode of the lateral branches, under the prophylls, the main axis always takes the place of the strong bud, the first hair-line being placed at the adaxial side.

WYDLER, describing the facts anew (73, p. 337) mentions the fact, that in floral branches the ridge lies in the direction of sepal 2. In itself this is nothing remarkable, as through the mode of calyx junction of most *Caryophyllaceae* sepal 2 lies above the SW divergence of the prophylls. In the actual specimens we see however that the hair ridge of an internode under a petiole, instead of coming to an end at the node above it, passes through the SW divergence and is continued along the whole petiole, abutting on sepal 2; as all flowers always bend towards the LW side, the hair-line of the curved petiole is turned towards the sky.

This fact is decidedly against the idea of the Bravais', and favours Wichura's view. Moreover the latter gets strong support from the fact, that quite similar hair-lines are present above the strong buds, as mentioned already by Wichura, in *Vincetoxicum*, and that in this genus the strong bud being subtended by the second leaf in the pair, the hair-line does not abut on the SW-, but on the LW-side of the higher node.

Of course the morphogenetic forces for the origin of the hair-line are quite unknown, but we may assume that they are connected in some way or other to the same forces to which the furthering of the strong buds is due.

2. The decussation of the involucre of *Dianthus*.

In *Dianthus*, as is well-known, an involucre of 2—3 pairs of sterile bracts is intercalated between the foliage leaves, or the prophylls, and the calyx. Of this involucre Eichler writes (20, II, p. 118) that in the case of a four-leaved involucre in an inflorescence branch he found "im obern Paar das erste Blatt (das theils durch die Deckung, theils durch den Kelchanschluss bestimmt werden kann) in den untersuchten Fällen immer auf Seite des α-Vorblatts (Fig. 41 C); sollte dies constant sein, so würde darin eine bemerkenswerthe Abweichung vom Verhalten der vegetativen Blätter sich äussern." For the reader's convenience the quoted diagram is reproduced here as fig. 17 A. He continues: "Denn bei diesen, sahen wir, sind die homologen Glieder der successiven Paare nach einer continuirlichen ¼ Spirale gestellt, so dass Blatt 1 des dritten Paares dem Blatte 1 des ersten gegenüber, erst Blatt 1 des fünften Paares wieder in dieselbe Richtung zu stehen kommt; hier bei den Involucralblättern aber erhält schon das dritte Blattpaar wieder die Orientirung des ersten und die homologen Blätter bilden somit nur 2, um einen R-Winkel abstehende Vertikalzeilen".

Some observations on *Dianthus plumarius* and *D. barbatus* showed that Eichler's diagram in fact is absolutely correct. The explanation however is very simple.

Eichler in determining the genetic order of the prophylls, relied on the general rule of the Caryophyllaceae that the β-prophyll subtends the strong branch. In the present case the involucre originally representing a short vegetative region, which

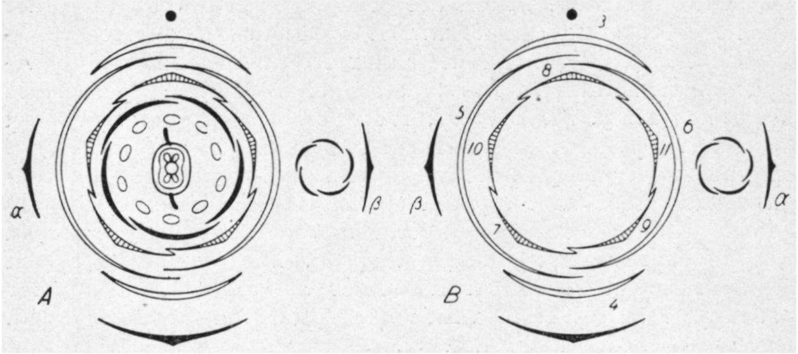

Fig. 17. *Dianthus plumarius,* A diagram of inflorescence branch, after Eichler (20, II, p. 106, fig. 41 C); B same with corrected indication of α and β and with numbering of involucre bracts and sepals.

has secondarily got into the sphere of influence of the flower, the prophylls are subject to the general rule of the *Caryophyllaceae* that in the vegetative region the first leaf of the pair subtends the strong bud, and so the diagram of fig. 17 A has to be changed into that of 17 B.

The correctness of this view may be proved already by the fact that when we trace back the calyx spiral in Eichler's diagram through the decussate part, α and β have to be interchanged. But moreover it is supported by the following fact. In *Dianthus plumarius* the main axis, on terminating in a flower, often produces a strong bud, in the shape of a flower, in the axil of one of the involucral bracts of the lower pair. This bud is always placed in the same ¼ spiral as all strong buds of the vegetative region; consequently the rule of the vegetative region also holds in the involucral part, and we may expect the same condition a fortiori in the prophyll region under it. The direct evidence for this condition given by the diagram in fig. 17 consequently is not to be doubted.

§ 14. Stellatae.

In the natural order of the *Rubiaceae* the *Stellatae* are remarkable for the clear traces of the original spiral in their binding whorls. In other *Rubiaceae,* though they are not nearly so well investigated in this respect, no doubt such traces are less frequent, often even absent.

Raciborski reports that in *Coffea arabica, C. liberica, Petunga Roxburghii* and *Sarcocephalus Junghunii* (41, p. 19) the axillary buds of the decussate whorls are of equal strength. On the other hand he describes decussate whorls with buds of different plastics, one being vegetative, the other an inflorescence, both arranged in ¼ spirals, in *Borreria ocymoides* and in *Spermacoce scaberrima* (41, p. 37, fig. 19): for *Spermacoce tenuior* WYDLER describes a ¼ spiral of the furthered buds (71, p. 375).

The narrower group of the *Stellatae* in one respect has decidedly a disadvantage as compared to the *Caryophyllaceae,* namely that the usually tetramerous and moreover strongly reduced calyx never reveals the original spiral. The vegetative region and the bracteal region on the other hand display a number of striking features from which the spiral can be determined. These features are the following.

1. During the developmental stages the two leaves of a pair may be of unequal sizes, as explained in § 10.

2. In the leaf pairs the SW- and the LW-side are often clearly to be distinguished by the convergence of the leaves. This follows from the observation by VON NÄGELI in *Galium Mollugo,* mentioned above, from the numerous observations by FRANKE (22), and indeed it may be observed easily in most *Stellatae.*

In *Galium Aparine* it is even the case in the cotyledons, and as the convergence of the cotyledons falls in the same ¼ spiral of the convergences of the plumular leaf pairs, we may distinguish between the first and the second cotyledon, both having a normal place in the spiral phyllotaxis.

3. The number of stipules in the LW angle is often greater than that in the SW angle. This fact, reported by VON NÄGELI, may for instance be observed in any specimen of *Asperula odorata, Galium Aparine* or any other species with seemingly polymerous whorls; as soon as we have whorls with 5 or 7 leaflets, as always occur between those with 4, 6 and 8, or occasionally even one with 9 leaflets, the odd stipule is placed on the LW-side. And there, where two successive whorls are odd-numbered, the course of the original spiral may be determined from their succession.

It is further remarkable that the convergence of the main leaves in these odd-numbered whorls usually is much more distinct than in even-numbered where it may be rather ill-defined. Evidently the larger available space first permits of the formation of a larger number of stipules in very young stages, and when this larger number has been once formed, it impedes in its turn the equalization of the angles which takes place to some extent in the other whorls.

This difference between odd- and even-numbered whorls shows itself as strongly in young expanding whorls as in adult whorls. Any one happening therefore to examine shoots with odd-numbered whorls in the adult region and even-numbered whorls at the top, may get the impression that the convergence of the two main leaves only arises during the last stages of growth.

This is the only way I can explain the observations by VON NÄGELI, who wrote: "Betrachtet man die Stammspitze von *Galium Mollugo* von oben, so scheinen die beiden obersten Blattanlagen genau den Enden des Durchmessers zu entsprechen und mit den beiden Blättern des folgenden Knotens ein rechtwinkliges Kreuz zu bilden. Aber meist schon die Blätter des dritten Paars sind etwas seitlich gerückt, indem sich die eine Hälfte des Knotens stärker entwickelt. Diese ungleiche Ausbildung wird weiter abwärts noch deutlicher" (37, p. 100). In fact shoots often have a series of whorls with numbers like 5, 5, 6, 6 or 5, 5, 4, 4 in the rising or in the falling part of their periodicity, and such shoots may easily have misled VON NÄGELI.

4. The SW- and LW-sides of the node may always be easily distinguished by the spatial relation between the axillary buds and the stem ribs.

As is well known the latter, being four in number, are a special feature of the *Stellatae*. They are lacking in the hypocotyl, in subterranean stolons (FRANKE 22, p. 42), and in the leafless parts of the inflorescence; as they are downward running ridges from the well developed leaves, their number diminishes in the inflorescence with the gradual progressive abortion of the leaves to 3, 2, 1 and finally to 0.

For the elucidation of their spatial relations to the buds we may refer to fig. 18, representing very schematically an unrolled surface of a stem piece of *Galium Aparine* with five nodes.

The four more or less equidistant ribs on the whole follow a longitudinal course, but as soon as a rib comes near to a main leaf insertion, it makes a rather sharp turn towards the SW-side of the node so as to reach the leaf insertion and the axillary bud.

Thus we only have to determine on which side of the rib the bud falls, to know where the SW-side of the node lies.

In fig. 18 the five whorls are seemingly heptamerous, two stipules being formed on the SW-sides, three on the LW. The ribs consequently pass between the stipules in the SW spaces, but in the LW spaces the middle stipule is inserted on the rib.

Wichura wrote in 1844: "Bei den Stellaten, mit welchen unsere Betrachtung beginnen soll, ist namentlich nicht bloss eine seitliche Convergenz der opponirten Zweige sehr in die Augen fallend, während dieselben bei einer diametralen Gegenüberstellung mit der Central-Axe in einer und derselben Ebene liegen müssten; sondern es erscheint auch der vierkantige oder wenigstens mit vier Riefen versehene Stengel sehr geeignet, uns von dieser Richtung der seitlichen Ausweichung auf das Leichteste Kenntniss zu verschaffen. Denn da von jenen vier Riefen ein gegenüberstehendes Paar in den Axillen der Hauptblätter verläuft, so hat man nur zu untersuchen, ob der Insertionspunkt eines Zweiges rechts oder links von der mit dem Mutterblatte correspondirenden Kante gelegen ist, und man wird die hiermit ausgesprochene Behauptung bewahrheit finden, dass bei den Stellaten stets der stärkere Knospenpunkt in der Richtung, und der schwächere wider die Richtung der beiden continuirlichen Spiralen von der Diametrale abweicht" (66, p. 193).

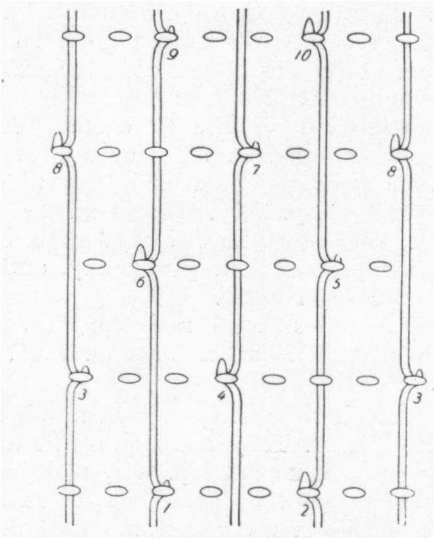

Fig. 18. *Galium Aparine*, schematic representation of stem surface, with course of ribs, insertion of leaves (numbered) and stipules, and position of axillary buds, for the case of homomerous whorls with five stipules each.

By our fig. 18 this somewhat obscure but otherwise excellent paragraph may be made clear, and we see at the same time that in the *Stellatae* it is really the second leaf which subtends the furthered bud.

The peculiar course of these ribs made **Wichura** believe that the thrusting aside of the higher stem part which is to be seen in the flower petiole, should also be present in the vegetative region: "Eben diese drängende Kraft der Zweige macht sich übrigens auch schon in den untern Internodien der Axe bemerklich, wo die in den Axillen der Mutterblätter entspringenden Kanten oder Riefen in der Richtung nach dem nächst vorhergegangenen stärkern Knospenpunkte bei Seite geschoben erscheinen" (66, p. 194).

This assumption no doubt is quite out of place here. The stem it is true often has a more or less pronounced bend just above the node, but this bend may as well be in the direction of the SW- as in that of the LW-side, or towards leaf 1 of leaf 2; it is simply due to a geotropical reaction, and has nothing to do with phyllotaxis.

5. In all *Stellatae* the leaves undergo a progressive simplification in the floral region. At first their stipules diminish in number and in size, till no more stipules are left. Finally the leaf which is itself also strongly diminished wholly aborts, the axillary product only remaining.

In the transitional regions we often find the leaves of a pair at a different stage of simplication, and then it is always according to their order in the original spiral; we may find a pair with only two stipules, both of the first leaf, or a pair of which only one lamina is left, that of the first leaf.

By all these different means we may prove that without any exception it is the second leaf of the pair which subtends the furthered bud. We may therefore be quite sure that the statement by **van Tieghem** that the buds arise in the axils of the first leaves (58, p. 361) is erroneous, and further that the "Anfangsblatt" of **von Nägeli** (see above § 10) is indeed the second leaf of the pair.

This having been stated three topics still remain to be discussed here, namely the aestivation of the leaves and stipules, the fusion of stipules and the change in the furthering in vegetative region and inflorescence.

1. According to **Franke** the aestivation in seemingly hexamerous whorls is a symmetric one (22, p. 54), the two main leaves being wholly overlapping, the two stipules of the "Anfangsblatt" of **von Nägeli** half overlapping, the stipules of the other main leaf wholly overlapped.

Some observations in *Asperula odorata* and *Galium Aparine* showed me that the aestivation in all polymerous whorls is subject to a great deal of variation; in *Galium Aparine* I once saw a seemingly heptamerous whorl which was wholly contort. Yet the main leaves very often are overlapping, and the stipules of the second leaf very often overlap those of the first leaf; the furthering of the bud from the second leaf evidently also influences the stipules of the latter.

2. The mode of fusion of the stipules of two leaves into an interpetiolar stipule has been discussed repeatedly, especially for the *Stellatae*, since EICHLER in his thesis of 1861 described an ontogenetic fusion of two separate primordia into one stipule, to occur regularly in seemingly tetramerous whorls.

From his observations on several species EICHLER wrote (19, p. 32): "Immer und in allen Fällen ist der Wirtel in seinen Jugendzuständen (mindestens) 6gliederig und es findet hier im Verlaufe der spätern Entwickelung eine ächte Verwachsung ursprünglich von einander getrennter Glieder statt".

The fact of such a regular fusion has been denied by GOEBEL (23, p. 231) who wrote that such a fusion at least occurs rarely, as in most cases the primordium from the very beginning is simple; and the same has been reported, from extensive investigations and as a rule without any exception, by FRANKE (22, p. 49).

When we compare the amount of alleged evidence, we cannot deny that GOEBEL and FRANKE are probably right and that an ontogenetic fusion will not take place.

The controversy however is not of great importance. In the case of a single interpetiolar stipule the prospective areas of the two stipules have united, have flowed together, before there is any bulging out of a primordium and even before the organization of the primordium has occurred.

In the case of two-topped stipules, described and figured in great number by TAKEDA (57), the fusion of the areas may have been completed, but the organization of the primordium originally has had two centres which united afterwards, and in the case of two separate stipules the fusion of the areas did not affect the primordium organization.

And when the *Stellatae*, as often occurs, from 3 or 4, sometimes even 5 stipules in one space between two leaves, the areas have fused first, just as is the rule in the *Rubiaceae* throughout; then the organization of the stipules begins with two primordia next to the leaves, and when the common area is large enough other primordia follow in between; in many cases a middle stipule is markedly smaller than the others.

The difference between EICHLER and GOEBEL is therefore that according to the former the fusion occurs during the visible stages, whereas if Goebel is right, it occurs earlier.

Takeda comes to the conclusion that for the *Stellatae* the tetramerous whorl is the primitive type, and that the hexamerous is due to fission. This view which very probably phylogenetically is correct, of course does not pertain to the ontogenetic processes and therefore is not to be taken into account here.

Pohl believes that the conception of a common interpetiolar stipular primordium presents considerable difficulties to logical thinking (40, p. 574). In the light of the above views this difficulty disappears.

3. The change in furthering mentioned above amounts to the fact that the bud from the second leaf being furthered in the vegetative region, it is the bud from *a* which is advanced in the inflorescence. So we may say that though being antipodal in their furthering, the *Caryophyllaceae* and the *Stellatae* are alike in the fact that they change on reaching the floral region.

§ 15. Apocynum, Nerium, Vinca and Lochnera.

The above genera are chosen as a very few representatives of the *Apocynaceae*, a family in which decussate phyllotaxis largely prevails, sometimes alternating with trimerous or polymerous whorls (*Alstonia*), sometimes with a phyllotaxis of the main series (*Amsonia*).

The binding character of these whorls, which already may be assumed from these facts (cf. Schoute 51, p. 678) is corroborated by the statement of Raciborski (41, p. 38) that the inflorescences in *Hunteria corymbosa* are placed in a ¼ spiral, and moreover by the fact that the nearly related *Asclepiadaceae* have the same binding whorls (cf. Schoute 53).

1. *Apocynum.*

According to von Nägeli (37, p. 96) the young leaves of *A. hypericifolium* are convergent in the buds and their leaf traces bend out symmetrically. Both facts point out the presence of an original spiral arrangement.

The same species, and especially another one, *A. venetum*, was studied by Zimmermann (86, p. 266—277). Both species showed leaf pairs with one weak and one strong bud, both arranged in ¼ spirals. The pairs were often more or less dissolved, and in the case of considerable level differences it was always the highest leaf that subtended the strong bud. In those pairs where the level differences were small, they were rather often such that the lower leaf subtended the strong bud, the ¼ spiral of the buds being undisturbed.

As judged by the level differences, the leaf spiral in such stem regious seemed to be reversed; ZIMMERMANN recognized however that this was only an apparent reversal, brought about by a longitudinal shift of the leaves.

In a third species, *A. androsaemifolium,* I found the lower leaf pairs strictly decussate, in the higher stem region the pairs showing very conspicuous convergences in a regularly ascending order. The buds of any pair being different in size, it was possible to state at once by the succession of the convergences that the second leaf of any pair subtended the strong bud.

The highest leaf pairs excepted, the level differences in the pairs were rather small or absent; the existing differences were often such that the first leaf was placed higher than the second.

These observations absolutely confirm those by ZIMMERMANN: the whorls are clear binding whorls, with irregular longitudinal shifts.

2. *Nerium.*

About *Nerium Oleander* WYDLER writes: Auf $^2/_3$ St. der Laubbl. folgt bisweilen $^3/_5$ St. der Hochblätter, wobei d. Kelch d. Gipfelblüthe d. vorausgehende St. unmittelbar fortsetzt". (82 p. 273).

From this statement it must follow that the spiral arrangement of the sepals is the continuation of the spiral, hidden in the trimerous foliage leaf whorls; my own observations confirmed this.

The branches in the flowering region always begin with one up to three dimerous and decussate leaf whorls, followed by three to eight trimerous ones; above the leaves 5 or 6, rarely 4 to 7, bracts and finally the terminal flower are formed.

The bracts usually are placed in dissolving whorls; the first three bracts often forming a more or less regular trimerous whorl, the higher bracts are always placed in a clear spiral.

In 17 examined branches the spiral of the bracts invariably was continued regularly in the terminal calyx.

3. *Vinca* and *Lochnera.*

The vegetative region of *Vinca* is strictly decussate; the axillary buds even do not betray the original spiral, as their development, though often unequal in the leaf pairs, does not follow any distinct rule.

In *Lochnera rosea* the leaf pairs are often clearly convergent, and if so, the narrow spaces ascending in a regular $\frac{1}{4}$ spiral give full information about direction and course of the original spiral.

In both genera any stem may end in a terminal flower, the calyx of which has a $^{2}/_{5}$ aestivation in the young condition; in *Lochnera* the spiral of the decussate part corresponds to the calyx spiral.

From the highest leaf pair two strong branches may be formed in *Vinca;* in that case the terminal flower keeps its central position. In the more common case where only one strong branch is formed we may state from the calyx aestivation that this branch is axillary to the first leaf. In becoming sympodial this branch throws the terminal flower into the axil of the second leaf.

In *Lochnera,* where the second leaf of the highest pair subtends a secondary flower, a sympodial branch is developed from the axil of the first leaf, and the terminal flower is displaced towards the LW-side, at about 45° from the second leaf.

The explanation of this peculiar interpetiolar position of the terminal flower has already been given earlier (53, p. 188) and may be read from our present fig. 19 in which two successive flowering nodes of *Lochnera* have been represented. The foliage leaves α and β have been indicated according to their original positions, not as they are placed later, and the arrows represent the shifts of the terminal flower under the influence of the two axillary buds, and the combined result of these two effects.

From the above follows that any flowering node apparently bears two flowers, one situated in the axil of β, the other inserted somewhat higher, at the LW-side. The main flower, being of an earlier generation, is much advanced in its development and opens first.

All sympodial branches in their turn end in a terminal flower; this may occur already after the formation of one single

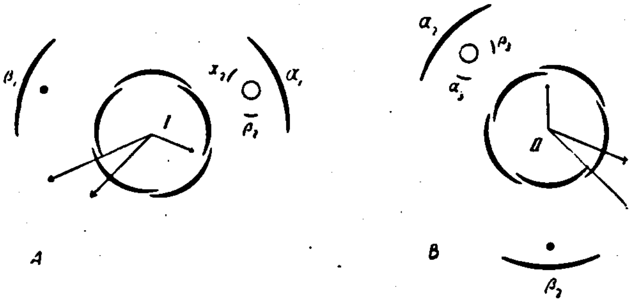

Fig. 19. *Lochnera rosea, A, B,* diagrams of two successive nodes of flowering region, the sympodium members having the most frequently occurring form of phyllotaxis. Leaves represented in their original positions; arrows indicate direction of shift of terminal flower; black dots in axil of β-prophylls = secondary flowers.

pair of foliage leaves, the prophylls (*Vinca major, Lochnera*), or after more pairs of leaves (*Vinca minor*). And as the successive sympodium members usually are homodromous, the flowers in *Vinca major* are arranged in a ¼ spiral and the inflorescence is a screw from α; in *Lochnera* the inflorescence is not only complicated by the β-flowers, but moreover the rectangular crossing of the leaf pairs is changed through the interpetiolar position of the main flowers into a skew crossing, as every sympodial member has its prophylls placed laterally with respect to the main flower of its parent axis.

From fig. 19 we may recognize already that the angular distance between two successive α-prophylls (or between two β-prophylls) is more than 90°, on account of the fact that the prophylls α_2 and β_2 are transverse with respect to their parent axis, i.e. flower I.

At some developmental stage both prophylls α_1 and α_2 are shifted to some extent, and so are the β-prophylls. These shifts are fairly complete, so that in the adult condition a complete opposition is sometimes reached, but often this fails by about 10° or 20° or even more. Yet, as the shifts of the homologous

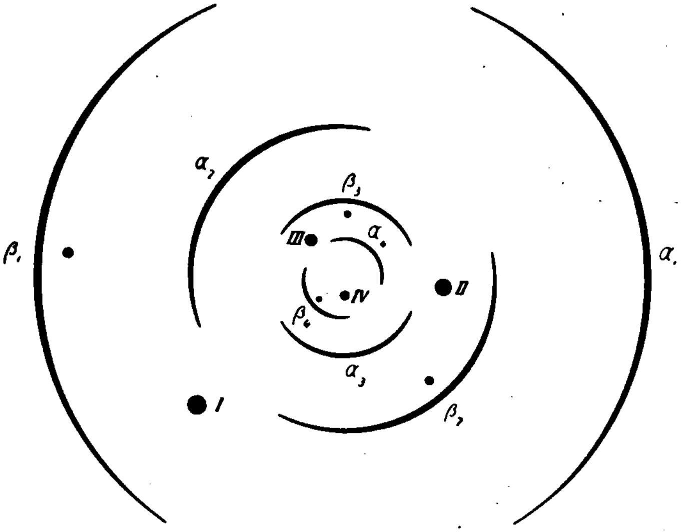

Fig. 20. *Lochnera rosea,* diagram of flowering region, the successive sympodium members all having the usually occurring form of phyllotaxis. Leaves represented in final positions. Dots in axils of β-prophylls = secondary flowers; I—IV = terminal flowers.

prophylls are in the same direction and of about the same extent, the distance α_1 and α_2 is not changed, at least not on the average.

The observation of some sympodia invariably showed me that mean distance α_1—α_2 is about 135°, or perhaps sometimes less, but not under 130°. This is shown by the fact that in any sympodium of sufficient length (fig. 20) β_4 lies right above flower I, or somewhat at the β_1 side of I.

At first this result seemed somewhat puzzling, as one might have expected that the angle would have been about 112.5°, on the following grounds.

In fig. 19 let the original divergence, as drawn, be 135°, then we have that α_1 and β_1 originally diverge over 22.5° from the opposed position. The big bud in the axil of α_1 shall therefore do likewise, and if α_2 and β_2 are placed symmetrically towards I, the distance α_1—α_2 has to be $90° + 22.5° = 112.5°$; and as remarked the subsequent shifts will not alter this relation materially.

A distance α_1—α_2 of 135° as observed would be conditioned only by an original divergence of 90°, and shifts of α and β consequently of 45°. As this is wholly inacceptable, it seems as if the theory is wrong.

We have however to bear in mind that I in fig 19 *A* is not only shifted by the influence of the strong bud from α and by α itself, but also by the flower from β and β itself. Accordingly in the adult condition I is shifted over an additional angle of about 22.5° (see 53, p. 188).

If now the bud from α_1 is organized at a time at which the terminal flower has already shifted, and if then its α_2 and β_2 are placed symmetrically towards it, the angle between α_1 and α_2 has to become about 135°. Conversely, the fact that this angle is of that size, makes it clear that the areas of α_2 and β_2 are induced at a time at which the area of I has already shifted.

The above description pertaining to the normal constitution of the flowering sympodia of *Lochnera,* we have still to mention that deviations may be due to differences in the course of the phyllotactical spirals.

In the first place we may observe that a sympodial member, though homodromous to its parent axis, has another way of beginning its spiral, α and β having inverse positions and the spiral running emprosthodromously from α to β. In that case the flower pairs ascend in a spiral with less than 90° divergence, with about 67.5°, and this spiral ascends in the reverse direction. The diagrams *A*—*C* in fig. 21 give two cases of such a succession.

In the second place a sympodium member may be antidromous to its parent axis, as in fig. 21 *D* to *C*. In that case the higher member will have its main flower at the other side of the β-flower and the flower pair spiral is reversed at the same time.

In the third place a foliage leaf whorl occasionally may be trimerous. This case is the more interesting in *Lochnera* as we may have then two strong branches, from α and from β, the third leaf subtending the secondary flower. The specimen, represented schematically in fig 21, in the fifth node *E* showed this condition, the third leaf here being much smaller, and the diagram illustrates that in such a case the terminal flower is shifted to the middle of the LW-divergence between α and β, the two strong buds having equal influences.

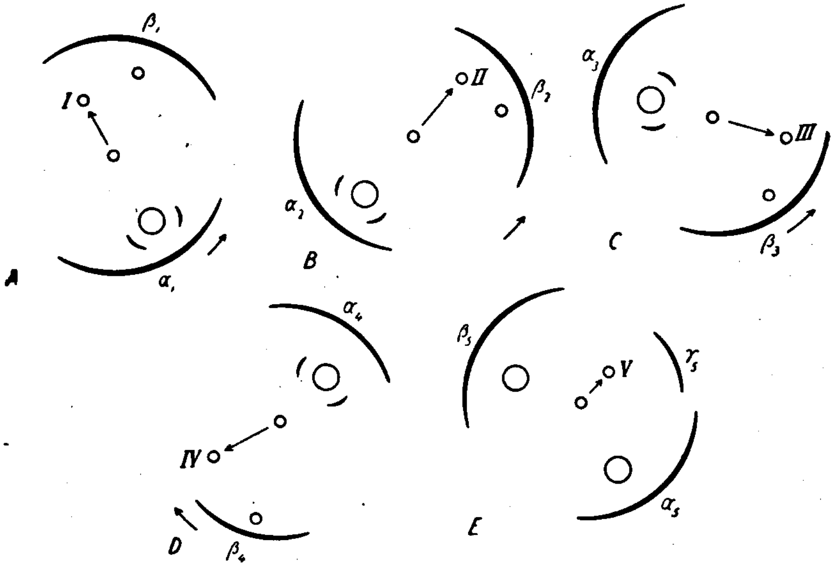

Fig. 21. *Lochnera rosea*, *A—E* diagrams of successive nodes of flowering region of particular specimen in which the sympodium members had different forms of phyllotaxis. Size of spaces between the leaf insertions drawn from the adult condition in nature. Arrows outside diagrams indicate direction of phyllotaxis spiral, arrows inside indicate shift of terminal flower. Strong buds from α_1 and α_2 (= II and III) homodromous to parent axis as usual, but with their α and β in the inverse position; bud from α_3 (= IV) antidromous, from α_4 (= V) normal.

From this description it may be recognized that the mode of branching in *Lochnera* to a large extent is analogous to that in *Asclepias* (53). Several authors on *Asclepias* or *Vincetoxicum* therefore have dealt with *Vinca* or *Lochnera* too, and we may even say that there is much in common in the course of the treatment of both topics in botanical literature.

As early as 1837 the Bravais brothers realized that the terminal flower in *Vinca rosea* (= *Lochnera*) is not thrown right into the axil of the β-prophyll, but on the LW-side, on account of the convergence of the two prophylls. They wrote: "que la fleur terminale semble extra-axillaire, son pédoncule étant déjeté vers la feuille-mère du pédoncule qu'elle termine, en vertu de l'inégalité des angles formés par les bractées géminées" (10, p. 322); a comparison with our fig. 19 will make clear that the terminal flower II is placed on the right of its seemingly subtending leaf β_2, towards the same side where a_1 falls.

They further knew that the second and younger flower of a flower pair is axillary to the β-prophyll; that those prophylls which are fertile in *Vinca parviflora* (= *Lochnera pusilla*) wholly abort (10, p. 42) and finally they knew that the angles between the successive flowers are more than 90°; "La spirale suivie par les fleurs autour du pseudothalle revient sur la verticale au bout de quatre pas environ sur le *Nerium;* mais sur le *Vinca* l'évolution circulaire est un peu plus rapide" (10, p. 323); and in the explanation of figures they add: "la spire formée ici par les fleurs du pseudothalle.... fait une révolution en trois tours environ" (ibid. p. 41).

By these observations the eminent authors gave a nearly complete explanation of the facts, the most important feature still wanted being the admission of the false whorl character of the decussate vegetative region.

Years afterwards Wydler independently explained *Vinca* in the same way and contributed several excellent new observations (75, p. 9), one of these being that below the terminal flower a half whorl sometimes may be observed (74, p. 630, 82, p. 272) and that in such cases the calyx spiral fits in with the unusual position of the leaf spiral.

At the end of his paper Wydler gave a postcript under the heading "Suum cuique", in which he quoted the Bravais'. About *Lochnera* Wydler did not give any comment, and this no doubt has been partly the cause that the excellent observations of the Bravais' on *Lochnera* have been entirely forgotten.

Eichler in his "Blüthendiagramme" of course accepted Wydler's explanation of the mode of growth of *Vinca* and gave a corresponding diagram of it.

It is however perhaps hardly necessary to mention the fact that this well-founded explanation of *Vinca* has been doubted by later botanists who were too much impressed by the outer appearance of developmental facts which were not understood.

So SCHUMANN wrote (21, IV, 2, p. 112): "Diese Deutung kann nur einen theoretischen Wert beanspruchen; der exacten Beobachtung nach entsteht die Bl. tief unterhalb des fortwachsenden, decussierte Blattpaare ausscheidenden Sprossgipfels als echter Seitenspross".

And CHURCH wrote (15, p. 191, footnote) in a caustic tone about the "elaborate cooking" which had been put forward by WYDLER and by EICHLER to explain "an occasional and isolated exception" by "trying to force the facts into one general scheme"; the explanation itself being "founded on purely academic reasoning" and being "perfectly gratuitous".

The basis on which these feelings are poured out is that there is "absolutely no trace of any such construction at the growing point at any stage of the development, the decussate symmetrical phyllotaxis being perfectly definite: in all respects the shoot behaves exactly as if the flowers were axillary".

Even if SCHUMANN and CHURCH had been right in contending that the terminal flower always arises in a seemingly lateral position under the new sympodial member, the alleged morphological facts would have been sufficient proof for the sympodial nature of the spurious axis, and we should have had only a new case in which the organs, at the moment in which they become visible as primordia, are already largely influenced by different morphogenetic factors.

But this is not the case. In the lower parts of a strong sympodium of *Vinca* the conditions evidently may be such as SCHUMANN and CHURCH describe them to be; in the higher parts of a sympodium it may be different.

WYDLER wrote: "Wenn wir auf die jüngsten Zustände von Laubspross und Blüthe zurückkehren, so lässt sich die terminale Stellung der Blüthe einerseits, die axilläre des Laubsprosses anderseits, nicht wohl verkennen" (75, p. 18). And in *Lochnera rosea* the same relation may easily be observed in the expanding parts, as I can confirm myself. Moreover DEMETER observed and pictured a terminal position of the main flower in *Lochnera rosea* in the first primordial stages (17, p. 135, fig. 2, 1 and 2, 6).

Descriptions of the morphological construction of *Lochnera* are rare in literature; after that given by the brothers BRAVAIS I only know of those by DEMETER and by WOODSON.

Neither of these brings any contribution to our knowledge, as they are made without a sufficient morphological basis.

Demeter writes that it is the younger flower of the pair which is subject to the lateral shift (17, p. 137), and Woodson describes not only descendingly serial flowers in the leaf axils, but moreover a cincinnus in *Lochnera* (85, p. 32), a contention which is paralleled by the remark that the bostryx is familiarly represented in the *Boraginaceae* (ibid. p. 5).

§ 16. Gentiana and Erythraea.

1. *Gentiana.*

Already in 1829 Schimper mentioned the ¼ bud spiral of *G. utriculosa* and *G. Pneumonanthe* (45, p. 86), adding that the pedunculus c. flore arises from the axil of the first leaf of every pair.

Later authors also make mention of this bud spiral: Wydler (68, col. 213, 74, p. 644), Irmisch (29, col. 691) and Irmisch adds that the subterranean axis of *G. Pneumonanthe,* being a short erect main axis with only scale-like cataphylls, produces its lateral branches, the overground leafy axes, also in a ¼ spiral.

My own observations only pertain to *G. Pneumonanthe.*

The decussate cataphylls of the subterranean main axis are highly connate, forming a tube with two short free apices, covering the tubes in the young condition and usually showing an aestivation.

According to Irmisch (29, col. 692) the cataphyll with the overlapping apex is the fertile one; Wydler on the contrary (72, p. 25) found that the overlapped cataphyll is the fertile one. Later (74, p. 647) Wydler wrote that on continued observation he also had found cases like those described by Irmisch, but with a smaller frequency.

In my own material the aestivation of the free cataphyll tips appeared also to be variable. It was however easy to show that in all cases it is only the first partner of the pair which has a furthered bud.

This was made possible by the fact that the two cataphylls, notwithstanding their complete connation, are clearly convergent, as their midribs are not opposed. The midribs of the successive cataphyll pairs even form a normal spiral, as may be seen in our fig. 22, no horizontal metatopies being discernible. The large axillary buds, being always placed exactly before one of the two midribs, appear to be axillary to the first leaf of the pair.

The large buds of this main axis grow out into the leafy

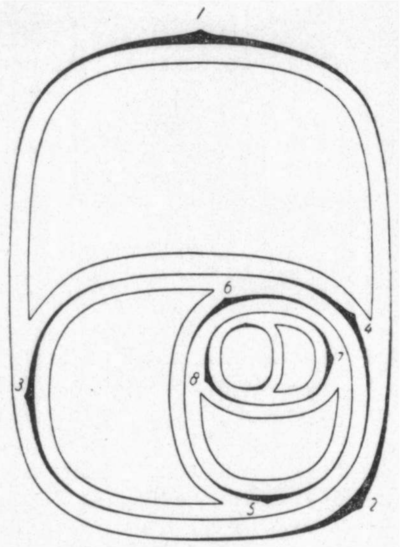

Fig. 22. *Gentiana Pneumonanthe,* phyllotactical diagram of subterranean main axis, with position of lateral buds. Midribs of connate bracts indicated.

shoots; the basal and subterranean part of such a shoot still forms about three cataphyll pairs which do not betray their original spiral. From the axils of these cataphylls similar leafy axes may arise, especially when their parent axis is damaged. These reparatory branches seem to arise indiscriminately from the two leaves of the pair.

Above the cataphyll region foliage leaves, and finally the terminal flower, follow. The higher pairs of these foliage leaves bear floral branches in a ¼ spiral.

As Wydler reports, the unequal length of the sepals sometimes indicates the calyx spiral (72, p. 25); from this we may determine the spiral in the foliage leaves and when doing so we find that the furthered bud comes from the second leaf, in contradiction to the statement of Schimper [1]).

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[1]) It is very curious that Wydler never made mention of the fact that Schimper was in error this time. Perhaps both awe and veneration for the irascible genius kept him back from doing so.

When in 1843 he wrote that in *G. Pneumonanthe* the bud spiral is subtended by the first leaves (68, col. 213), he may have simply quoted Schimper. But when in 1860 he described the junction of the terminal flower to the leaf pairs, of which he determined the phyllotaxis by the bud spiral (74, p. 648), he must have been aware, as far as I see, of the real state of things.

But as the sepals often are about equal in length, a better criterion for determining the original spiral is needed and this is afforded by the convergence of the higher foliage leaves.

On the internodes two free leaf cushions are decurrent from the leaf insertions; the two spaces between these cushions being unequal, we can easily state that the narrow spaces ascend in a ¼ spiral, which is homodromous to that of the furthered buds and precedes them.

From this fact it follows unmistakably that the second leaf is fertile, and accordingly the spiral determined in this way corresponds to that observable sometimes in the terminal calyx; in the highest leaf pair the sterile partner lies below sep. 4, the fertile one below sep. 5, as might be expected.

As the wide space between the two leaf cushions, on the LW-side, lies above the furthered bud of the lower leaf pair, one might suppose that the wide space would be due to the mechanical influence of the large bud body. But in such exceptional cases in which the two buds of a leaf pair are both strongly developed, the same difference in the spaces between the leaf cushions subsists.

In two specimens further evidence for the correctness of the leaf spiral so determined was furnished by the development of a half whorl, an odd leaf, under the terminal flower. In both cases it was situated above the strong bud in the highest dimerous whorl but one and under sep. 5, as might have been anticipated.

2. *Erythraea.*

In 1844 Wichura mentioned a "continuirliche Spirale" of the buds for the *Gentianeae;* amongst the instances *Erythraea spicata* is given (66, p. 181). Wydler in 1860, though mentioning the fact that in *E. spicatum* and in *E. Centaurium* usually only one leaf of every pair is fertile (74, p. 651), is silent on the succession of the strong branches.

In my own observations, which only pertain to *E. Centaurium,* this succession was found to be strikingly irregular, in some cases the third node having a strong branch above that of the first node, in other cases only the fifth node having it.

For a closer investigation it was a great advantage that in the higher leaf pairs very clear convergences were present, ascending in a ¼ spiral. These convergences were to be seen from the spaces between the leaf cushions on the internode, from the positions of the leaves themselves and from the directions of the lateral branches; the original leaf spiral as revealed in this way perfectly corresponded to that as given by the calyx aestivation of the terminal flower.

In this way I found that in 8 main stems 12 branches arose from the first leaf of the pair and 31 from the second. By the irregular mingling of these two kinds of branching one and the same stem might show a region with a $\frac{1}{4}$ spiral of the strong branches and in another part a zigzag of the strong branches; the longest stem part of both forms comprising six consecutive nodes.

Our conclusion therefore may be that there is a stronger tendency for the bud from the second leaf to develop, but it is far from dominating. For the assumption of a slight dorsiventrality causing a zigzag development of the branches there are no arguments.

In the greater frequency of branches from the second leaf the close relation to the genus *Gentiana* may find expression.

Half whorls between highest leaf pair and terminal flower were observed in a few cases, always in the due position.

§ 17. Blumenbachia and Cajophora.

1. *Blumenbachia Hieronymi.*

In the adult parts the stem which is monopodial throughout, is strictly decussate.

One of the leaves of every pair subtends a small vegetative bud; these buds ascend in a $\frac{1}{4}$ spiral. The other leaves each subtend a single well-developed flower, with two small lateral prophylls at the end of the long flower stalk.

At the shoot apex the young leaves clearly converge. The SW-sides ascend in a homodromous $\frac{1}{4}$ spiral, and as the flowers are already discernible in the very young stages, it becomes clear that the first leaf of every pair subtends the vegetative bud, the second leaf the flower.

2. *Cajophora lateritia.* In the vegetative region the two buds of a leaf pair are very unequal in size, the strong buds ascending in a $\frac{1}{4}$ spiral and coming from the first leaves.

As there is no convergence in the leaf pairs, the proof for the latter statement had to be derived from cases with dissolved or with half whorls.

Fig. 23 *A* represents a particular shoot in which the leaves 1—10 are arranged in normal decussate whorls, with clear $\frac{1}{4}$ spirals of the strong and the weak buds. The sixth whorl is dissolved and consists of one foliage leaf 11 and a much higher phyllome with the shape of a sepal. The calyx of the terminal

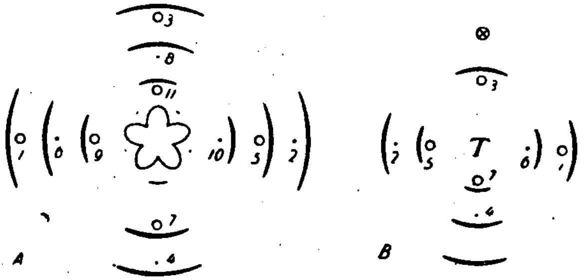

Fig. 23. *Cajophora lateritia. A*, diagram of lateral shoot with five normal dimerous leaf pairs, the sixth consisting of one foliage leaf and one much higher inserted very large sepal; the calyx just over this sepal has one open space. Strong buds in a ¼ spiral, including leaf 11. *B*, similar shoot with three normal leaf pairs and one odd leaf under the terminal flower T. Strong bud spiral includes leaf 7.

flower is inserted 2 mm above this large sepal and consists of four normal sepals, leaving one place open over the large sepal.

Another shoot showed a solution of a foliage leaf pair, the lower leaf lying in the spiral of the strong buds, the higher leaf being inserted 5 mm higher. The stem in this shoot bent away from the leaf at the insertion of both single leaves as described above in § 6.

Some other shoots showed the condition represented in fig. 23 *B*, where a half whorl has been formed under the terminal flower, the odd leaf in all cases lying in the strong bud spiral.

All these cases give proof that really the first leaves of the pairs subtend the strong buds.

The opposed buds from the second leaves do not grow out into a flower as in *Blumenbachia,* all flowers here being terminal. The first flower once being formed, the strong bud from the first leaf of the highest pair develops a pair of leafy prophylls and then ends in another terminal flower, and so on. The successive flowers form a cincinnus which according to EICHLER is from β; consequently we have here another case of the same change in branching method as in the *Caryophyllaceae,* from the first leaf in the vegetative region, from β in the inflorescence. The difference with the related monopodial *Blumenbachia,* at first so striking, on second thought therefore is less than it seemed to be: the strong vegetative buds in both are from the first, the flowers from the second leaf, the difference being that the two processes are combined in one region in *Blumenbachia,* and separated into two different regions in *Cajophora.*

Note. The inferior ovaries of *Cajophora lateritia* being straight, the capsules are twisted and, as in the other species of the section *Dolichocarpae* and those of the sections *Platypetalae* and *Bicallosae,* the twist in the cincinnus is alternately to the right and to the left, whereas the species of the sections *Angulatae* and *Bialatae* have all fruits twisted to the right, like those of the genus *Blumenbachia* (see 21, III, 6a, p. 119).

This interesting case of auto- and heterotropic twist (for the meaning of these terms see 49, 50, 52) fully deserves a special investigation. With the material at hand I could only determine that if EICHLER is right in contending that sep. 2 of any flower is turned towards the parent axis, the phyllotactical spiral of the flower and the fruit twist are homodromous.

§ 18. Mercurialis perennis.

In § 9 it has been mentioned that AL. BRAUN gave a description of the phyllotaxis of *Mercurialis perennis* from which was to be assumed that the original divergence of the spiral phyllotaxis must have been 150°. The same is to be gathered from the statement by WYDLER that between the obliquely crossing leaf pairs the divergence is $^2/_6$ (80, p. 27).

My own investigation gave the following results.

The vegetative branches, arising from the subterranean stolons, bear clearly convergent leaf pairs. Between two leaves the two stipules which are inserted separately on the stem (stipulae caulinares, see WYDLER 80, p. 27) are nearer to each other on the SW-side than on the LW-side; when they are still erect on the SW-side they may already be spreading or even downwardly inclined on the LW-side.

These SW-sides ascend in a regular spiral the divergence of which is more than 90°, something like 100°. This fact already proves that the original divergence is more than 135° and must be near $(180° + 100°) : 2 = 140°$.

The young expanding leaves are of distinctly unequal sizes in the leaf pairs, and on determining their order in the spiral from the convergences, we always find that the second leaf of the pair is smaller. As an instance the leaf lengths of a particular specimen may be given, for leaves 5—14; 5—10 being fully grown. They were successively 7.7, 7.2; 8.4, 8.6; 7.5, 7.0; 5.2, 4.6; 2.2, 1.6 cm.

For a more exact determination of the original divergence we can make use of the fact that the stem has two prominent ribs on every internode, the upper end of which lies right between two stipules, the basal end lying in a leaf axil. These basal ends never lie in the median plane of the subtending leaf, but in a given specimen they all either lie to the left or to the right of that median plane, according to the skew crossing of the leaf pairs.

On following the original longitudinal course of the cell rows, by means of these stem ribs, over four internodes, I found that the ninth leaf is situated at the anodic side of the first, the secondary divergence of the ninth leaf being between 60° and 80°. This amounts to an original primary divergence between 142.5° (for 60°) and 145° (for 80°).

An original divergence of 150° as would follow from the observations by Braun and Wydler, would imply that the secondary divergence of the ninth leaf should have been 120° which was certainly not realized in my material.

§ 19. Casuarina sumatrana.

Raciborski mentions for *Casuarina sumatrana* (41, p. 38) that in the tetramerous whorls every node bears only one bud, the buds of successive whorls being arranged in a $3/8$ spiral.

Such a distribution may be the consequence of the formation of binding whorls out of a spiral of the main series (see fig. 5 *A*), if in all whorls a homologous leaf, for instance the first or the last, is fertile. The successive divergences of the spiral through the horizontal metatopies in such a case are changed into 180°, 90°, 180°, 135°, 180°, 90°, 180°, 135° etc.

In order to investigate this remarkable case I examined material from the same species, received from 's Lands Plantentuin in Buitenzorg.From a single branch system I determined the bud spiral in 150 branches, 75 of which were secondary and tertiary branches, the main branch being supposed to be a primary branch, whereas the other 75 examined branches were of quaternary order.

In all these 150 branches the first whorl consisted of a pair of lateral prophylls and the second whorl of four leaves, placed diagonally. On this second whorl followed an indeterminate number of alternating tetramerous whorls, in the vegetative region as well as in the strobilus-like inflorescences.

The occurrence of a single dimerous whorl at the beginning must be due to an initial variation in the regular order of the binding, and the divergences in the adult state cannot be an endless repetition of 180°, 90°, 180°, 135°, but the first two divergences have to be different; the most probable supposition is that they are 180°, 135°.

As the spiral in the system may be dextrorse or sinistrorse and as it may run opisthodromously or emprosthodromously from α to β, there are four possible forms of the system, two of which have been represented in our fig. 24 as RE (right spiral, emprosthodromous) and RO. The two mirror-images may be indicated as LE and LO.

For a further investigation it would have been requisite for the observed conditions to be compared with other traces of the original spiral. But as these could not be discerned, I tried to make the best of it by the following indirect mode of investigation.

In all branches the bud spirals were determined and their course was noted down. As the bud spirals were realized with an astonishing accuracy, this was very easy. The dimerous and the first tetramerous whorl were always sterile, and sometimes one to three further tetramerous whorls. The higher whorls usually had one single bud, only in thin branches was one or more whorls in an irregular order sterile. This did not influence the course of the spiral which continued its way higher up as if the empty places had been filled. It was only once that I saw a whorl with two buds, a stronger one in the right place and a supernumerary one in the axil of the leaf to its left.

To make the different cases comparable, all bud spirals were supposed to begin in the third whorl, missing buds being imagined present. This having been done the cases could be classified as follows.

Bud spiral:	right-handed		left-handed	
Observed in:	Sec. and tert. br.	Quatern. branches	Sec. and tert. br.	Quatern. branches
First bud front side	8	1	12	1
„ „ back side	0	0	0	0
„ „ left side	11	7	18	42
„ „ right side	19	22	7	2
	38	30	37	45

These figures in their distribution are remarkably irregular. When we compare them with our fig. 24, we see that first bud front side and left-hand bud spiral must be realized when in a phyllotaxis of the form RO the last leaf of every whorl is fertile (10, 14, etc.). If we call this "RO from 10", the other observed forms are from the same assumptions:

Bud spiral:	right-handed	left-handed
First bud front side	= LO from 10 (n = 9)	= RO from 10 (n = 13)
„ „ back side	= LE „ 10 (n = 0)	= RE „ 10 (n = 0)
„ „ left side	= LE „ 7 (n = 18)	= RO „ 7 (n = 60)
„ „ right side	= LO „ 7 (n = 41)	= RE „ 7 (n = 9)

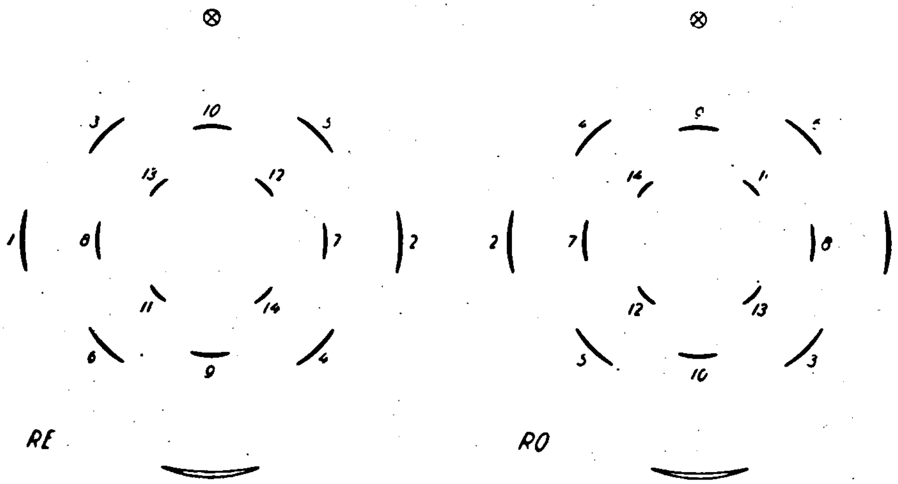

Fig. 24. *Casuarina sumatrana.* Two possible forms of diagram of phyllotaxis of lateral branches; RE right hand leaf spiral, running emprosthodromously from 1 to 2; RO same but opisthodromous.

As we see the opisthodromous forms largely prevail (123 agains 27). At the same time the great majority of the branches seem to bear their buds in the axil of the first leaf (128 against 22 cases).

As to the first result there is no objection to taking it for granted, as a predilection for a certain course of the genetic spiral is a very common phenomenon in Dicotyledons. The other result however can hardly be accepted as such. For if there is a certain rule for the distribution of fertility in the whorl according to the age of the whorl members, as is undoubtedly the case here, it is extremely improbable that this rule will be reversed in some branches of the same plant.

There may however be another solution of this problem. Above we supposed that the original divergences were transformed in to 180°, 135°, n (180°, 90°, 180°, 135°). Now it may be that in the beginning the rule may vary, and that according to one of the complex formulae of VON NÄGELI (§ 2) a single divergence of 45° is inserted, either between leaf 2 and 3 or between leaf 6 and 7. Fig. 25 represents these two cases for a RE pattern. As we see in these diagrams the first leaf of the third whorl falls on the front side, and the 22 deviating cases may have been due to such a form of phyllotaxis.

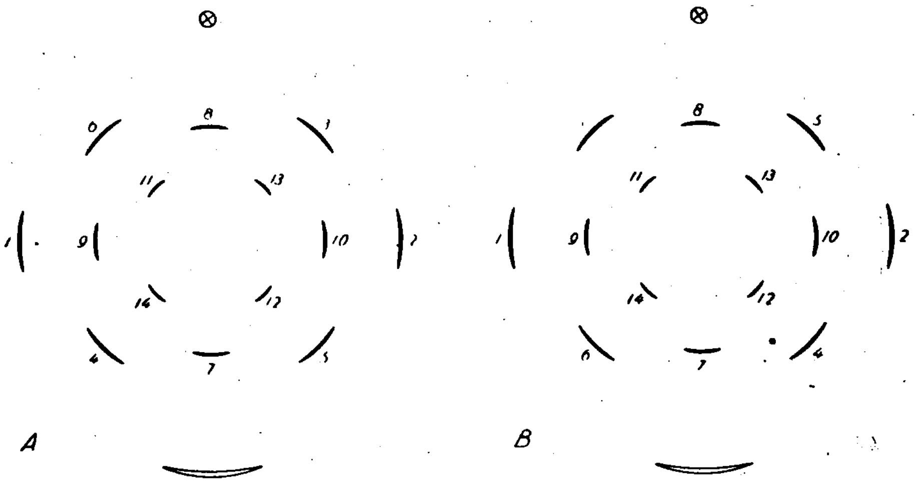

Fig. 25. *Casuarina sumatrana.* Two other possible forms of diagram of phyllotaxis of lateral branches, only different from RE in fig. 24 by the fact that one of the divergences of 135° has been substituted by a divergence of 45°.

Of course this is all very hypothetical and it would need further research before it could be accepted. Yet we may consider it as established that the tetramerous whorls of *Casuarina sumatrana* are binding whorls, derived from a system of the main series, and moreover it is highly probable that it is the first leaf of every whorl which subtends the bud.

§ 20. Acer platanoides.

The bracts on the main axis of the inflorescence of *Acer platanoides* according to AL. BRAUN have a phyllotaxis of $(\frac{1}{2})\ ^{2}/_{6}$, as reported above in § 9.

So the leaf pairs seem to have been formed in a spiral system with the unusually large divergence of 150°. Accordingly the case was submitted to a renewed investigation.

The inflorescence in this species is terminal to relatively short lateral branches, especially in their second or later year. The mixed bud from which it comes is covered by a number of strictly decussate bud scales, and contains moreover one or two pairs of strictly decussate foliage leaves.

Above the foliage leaves from 6 to 10 bracts are formed, followed by a terminal flower. These bracts are clearly convergent in the pairs and moreover the pairs are often more or less dissolved.

The SW-sides which ascend in a ¼ spiral enable us to determine the original spiral;all notable differences in level then appear to fit in with the leaf numbering.

Above the last bract pair a terminal flower is produced.

In the case of 10 bracts the position of the fifth pair was compared with that of the first, in the case of 8 bracts the position of the fourth pair with that of the highest foliage leaf pair. In all cases it was found that the fifth pair was not situated over the first, but that it diverged towards the anodic side by an angle which could only roughly be measured by following the epidermis lines, and which was between 45° and 90°.

The original divergence in the spiral accordingly may have been something like 143°, as a secondary divergence in the octonary parastichies of 45° corresponds to a divergence in the genetic spiral of 140⅝° and one of 90° to 146¼°.

§ 21. Fraxinus.

A study of the binding whorls in *Fraxinus* is the more required, as the genus has played an important rôle in the literature on decussation, so much so that dorsiventral decussation has been called the "Decussation der Fraxineen" (SCHWENDENER 54, p. 85).

Since in the present paper *Fraxinus* is treated in a chapter on radial binding whorls, this implies that the present author does not include the phyllotaxis of *Fraxinus* in the dorsiventral systems: a justification of this view may follow.

Already in 1829 SCHIMPER remarked that the first leaves of the pairs are arranged in *Fraxinus* in a zigzag, and that they all fall into two of the four orthostichies. This fact which was stated from the frequent solutions of the dimerous whorls has been the argument for later authors to consider the phyllotaxis of *Fraxinus* as being dorsiventral.

Yet it was already known to DUTROCHET in 1834 (18) that the phyllotaxis in *Fraxinus* may vary, especially in gourmandizers, and that the dimerous whorls may be dissolved in two different ways, in the seemingly dorsiventral form described above, and in the direction of radial systems, the fifth pair being the first to have the same position as the first. Moreover other branches may have a complete transition to a $^2/_5$ spiral.

Such a variation is a rare phenomenon in a plant with truly dorsiventral shoots. And if we then consider the fact that neither the leaves of a pair nor the buds ever show any other phenomenon of dorsiventrality (WYDLER 82, p. 54), the so-called dorsiventrality becomes more and more problematic.

Moreover our doubt grows when we read in WYDLER about *F. excelsior* (74, p. 628): "Die Blattstellung gewöhnlich opponirt-decussirt, aber die Paare sowohl in der Laub- als Hochblatt-Region häufig mit Beibehaltung der Decussation aufgelöst, wobei dann am öftersten die ersten Blätter der dritten Paare über einander fallen, aber auch viele Unregelmässigkeiten vorkommen".

Apart from the absence of other dorsiventrality phenomena it was especially these irregularities which required a renewed investigation, and so I examined in detail the phyllotaxis of normal branches as well as of gourmandizers of several ash trees. The outcome may be summarized as follows.

In the ordinary rather slowly growing branches of a normal tree most leaf pairs are strictly opposed without any solution; in rapidly growing main branches and especially in gourmandizers solution is very frequent, at least in the foliage leaf pairs. The bud scales on the other hand are always exempt from solution.

In inclined or horizontally growing branches the solution, where present, follows the rule that in those pairs which are placed on the upper and under side of the shoot the under side leaves usually are shifted towards the branch apex; opposite shifts, even over some cms are always to be found, in *Fraxinus excelsior* as well as in *F. Ornus*.

Another rule is the following one. When in any branch, whether inclined or erect, a leaf pair is dissolved, the next higher superposed pair usually has a level difference in the same sense: hence the zigzag of the first leaves. But when we follow an orthostichy over a certain length, we see that after a varying number of leaf pairs the difference disappears or is reversed. An intervening bud scale zone does not influence the phenomena in any way, a level difference often being resumed over the bud scales in the same sense.

As the changes in an orthostichy might be connected with a different position with respect to gravity, light or any other outward stimulus, a number of erectly growing gourmandizers was investigated and the slight torsions of the orthostichies were carefully taken notice of. In these five year old branches, grown from the stumps of a series of cut ash trees and having 60 to 75 leaf pairs in an uninterrupted sequence, the orthostichies from beginning to end deviated, sometimes with oscillations, at least 40°, at the most 240°. In these branches no correlation whatever was found between the inversion of the solutions and the orientation of the branch region towards the points of the compass; the inversions occurred in branch regions without as well as in those with stem torsion, and a branch with a total torsion of not yet 180° might have three or four changes in the solution direction of two opposed orthostichies.

As every change in the solution direction has the consequence that three leaf pairs have their first leaves in a ¼ spiral, those places where two or more inversions were near together might have a ¼ spiral through several pairs. In the five gourmandizers which I examined the longest stem piece with a ¼ spiral comprised 6 leaf pairs; the longest piece with a zigzag of the first leaf on the other hand comprised 20 pairs, i.e. 14 pairs of dissolved leaves and two intervening bud scale zones with 3 pairs each.

On the basis of these facts I am inclined to assume that the decussation in *Fraxinus* is perfectly radial, but that by some kind of coherence of the leaf insertions, or their traces, the leaves of an orthostichy are united, so that a shift in a vertical direction of a given leaf may be repeated in the same sense in the next leaf above it in the same orthostichy; there is no need to remark that such a coherence has nothing to do with dorsiventrality.

In addition to the ordinary cases of decussate shoots, one single gourmandizer was examined with 59 consecutive trimerous whorls. The phenomena were all perfectly analogous, but as there are six possible variations of the insertion level in a trimerous whorl and only two in a dimerous one, the stem pieces with a uniform succession of level differences were shorter here, the longest part with a strict zigzag of the higher, the middle and the lower leaf comprising only four whorls, and the longest part with a spiral succession only three whorls.

Shoots with a spiral phyllotaxis throughout, as mentioned by DUTROCHET and by WYDLER did not occur in my material. The latter author wrote: "selbst die Laubblätter in mehreren $^3/_8$ Cyklen gestellt, habe ich mehrere Male gefunden" (74, p. 628). This fact is not against the assumption that the whorls are binding whorls, as there may always be cases in which the whorl forming factors are less active or even lacking altogether.

§ 22. Rhamnus cathartica.

A branching system of *Rhamnus cathartica* consists of typical elongated shoots, typical dwarf shoots and all transitional stages between these two kinds of shoots.

The dwarf shoots and all rather slowly growing elongated shoots have a decussate phyllotaxis, the rapidly growing elongated shoots at least in their apical part usually being spiral.

In the decussate shoots the leaf pairs are often dissolved in a rather irregular way, the lower leaves being neither placed in a ¼ spiral nor in a zigzag.

In order to examine this curious arrangement we may look at elongated shoots with a decussate basis and a spiral upper part; by tracing back the spiral from above, the whorl solutions may be classed as eutopic and metatopic shifts.

In doing so it appears that both kinds of shifts occur: in an erect pseudoterminal branch 18 whorls were followed by 5 leaves in a clear left spiral. In the whorls 5 of the shifts were eutopic, 7 metatopic, in an irregular succession; whorl 11, 14, 15, 16 and 18 having eutopic, 4, 6, 8, 10, 12, 13 and 17 having metatopic shifts.

Now it might have been that the solutions were due to a dorsiventrality of the shoot, in which case both eutopic and metatopic shifts must occur, but the above example is already against such a supposition, as all leaves of the same orthostichy in such a case must have the same shift, so that every third whorl would have the same slope.

From some decussate branches I therefore determined the correspondence in slope of successive superposed whorls; I found that against 37 cases of correspondence there were 21 where the two whorls had an opposed slope direction. This result is the more curious as the successive superposed whorls should all have alternating slopes in the case of eutopic solutions.

Now one might still suppose that the solutions were due to the influence of a unilaterally acting factor like light or gravity, but that the four longitudinal leaf rows were more or less winding, either through torsion or through not being true orthostichies; in such a way the outside factor would act differently in the different parts of one and the same longitudinal leaf row.

To a certain extent such windings really were to be observed, but at the same time it was evident that the solutions could not be conditioned by some outside factor, as there was no correspondence between the position of the branch and the solution direction. In horizontal branches for instance the vertical leaf pairs might have their under leaves shifted in the apical as well as in the basal direction.

So the only remaining possibility seems to be that the leaf pairs may be dissolved as in *Fraxinus* by some kind of coherence in the longitudinal leaf rows, and perhaps moreover sometimes by a persistence of the original spiral.

Such a coherence must give rise to a metatopic shift in one of any two cohering leaves and at the same time to a similar slope in superposed pairs.

Rhamnus cathartica is mentioned by Wydler amongst the species with a dorsiventral type of decussation (84, col. 822). This may be based on the observation of parts of shoots in which the solutions were all in the same direction, such as Henry had already figured (27, p. 276, pl. 25 fig. 20); of course another possibility is that different forms or races of the species may differ in this respect; in view of the fact that *Rhamnus Frangula,* to be described in § 33, is clearly dorsiventral such a condition would not be amazing.

On another occasion (73, p. 456) Wydler describes the seedlings of *Rh. cathartica* as having either directly spiral plumular leaves or beginning with one to three decussate pairs after the cotyledons before the spiral sets in.

§ 23. Salix purpurea.

The descriptions of the phyllotaxis of *Salix purpurea* in literature being remarkably contradictory, a new investigation was needed.

The only two instances Schimper gave of a decussation with a zigzag position of the first leaves were *S. purpurea* and *Fraxinus:* he wrote (45, p. 88) that in *Salix* the leaf pairs, though being clearly recognizable, are often dissolved, in the way indicated.

Henry added the fact that many branches have a distinct spiral (27, p. 329). Concerning the solutions of the leaf pairs of the decussate branches he wrote that the first leaves are nearly always placed in a $1/4$ spiral and that the only exceptions he found were combinations of $1/4$ spiral and zigzag; a diagram represents a shoot (p. 333) with three leaf pairs with a left-hand spiral, followed by three other leaf pairs with a homodromous but opposed spiral, so that the first leaves of the second to fifth pair form a zigzag.

In view of the discrepancy between his observations and those of Schimper he concludes that the phyllotaxis is not governed by a fixed rule.

In 1870 Wydler wrote (81, p. 253) that he had observed both modes of solution mentioned by Schimper and Henry, further numerous spiral shoots and moreover other anomalous arrangements which he considered to be metatopic.

My own observations showed me that all branches after the two superposed lateral leaf pairs, described by Henry, form a varying number of decussate pairs, which may be followed by a spiral region, especially in rapidly growing shoots; this spiral part may extend over more than 50 leaves and is quite regular.

The decussate parts have many irregularities and whorl solutions; the four longitudinal leaf rows may wind more or less and certainly do not occupy a fixed position towards gravity or light.

No rule was to be discerned in the distribution of the solution direction. Out of 63 cases of superposed leaf pairs the level difference was in the same direction in 37, in opposed directions in 26 cases; the longest piece of shoot with a spiral arrangement of the lower leaves bore six, the longest piece with a zigzag arrangement four leaf pairs.

Our conclusion from these observations may be that the distribution of the whorl solutions does not furnish any argument for the presence of a crypto-dorsiventrality in the apparently perfectly radial shoots. No more is there any argument for a coherence of superposed leaves, such as was assumed in *Fraxinus;* both factors woud have brought about a preponderance of a parallel slope in superposed whorls.

The solutions not being eutopic throughout either, their haphazard distribution seems to be ruled only by chance, i.e. by a number of unknown and varying factors.

In any case we have to take the whorls as a radial system; that they are binding whorls is already made very probable by their numerous transitions into regular spiral systems, and it is moreover corroborated by the following observation.

A particular shoot drew the attention by being spiral in its middle region only. Four lower whorls were strictly decussate with hardly any solutions, the next eight leaves were regularly spiral so that no pairs were to be recognized, and they were followed by two whorls with a rectangular crossing and small level differences. Such a return to decussation can only easily be understood in binding whorls.

§ 24. Helianthus annuus.

The phyllotaxis of *Helianthus annuus,* having been investigated by numerous morphologists, might be supposed to be so well known as to leave no room for further investigation.

Indeed hardly any author on phyllotaxis will have omitted to pay attention to the conspicuous and very regular systems in the large flower heads, especially in the fruit stage; several authors described them in their papers. Thus for instance Schimper (45, p. 111), the Bravais' (9, p. 67, 87), Braun (7).

From their descriptions it is clear that the parastichy numbers of the paleae in the heads usually belong to the main series, being 21, 34, 55, 89, 144 or 233; in exceptional cases they belong to some other series.

Weisse found moreover that in those cases in which the flowers are arranged according to the systems of the first accessory series, the same system occurs also in the higher foliage leaves, in the shape of a $^2/_7$ pattern (65, p. 464); finally an analysis of the phyllotaxis of the whole main stem has been given by Church (14, p. 109).

The decussate stem base was considered by these authors to be a region with an entirely different form of phyllotaxis, a form only related to the patterns of the higher regions in the case of parastichies belonging to the first jugate series. For us however this decussate region is of a secondary origin, due to the action of the binding factors, and the transition to the different systems higher up is nothing but the inactivation of this binding.

Thus the transition zone receives an additional interest, and the question particularly arises how such a transition takes place in the rare cases of anomalous phyllotactical series in the higher stem region.

As these exceptional series can easily be obtained by growing a sufficient number of specimens, some hundreds of plants were raised from seeds in 1937 in the Groningen Hortus; only the main stems were investigated, no lateral branches.

For the determination of the phyllotaxis observations were made in various developmental stages; as the cotyledons die away early, their position was noted down for any seedling and even the position and distribution of the lower foliage leaves was recorded for every separate specimen.

Tricotyledonous or other anomalous embryos not occurring in the cultures, all specimens were similar in having two cotyledons.

In the foliage leaf region longitudinal shifts occurred sometimes, rendering uncertain the exact determination of the phyllotactical system. So the flower parastichies were always counted,

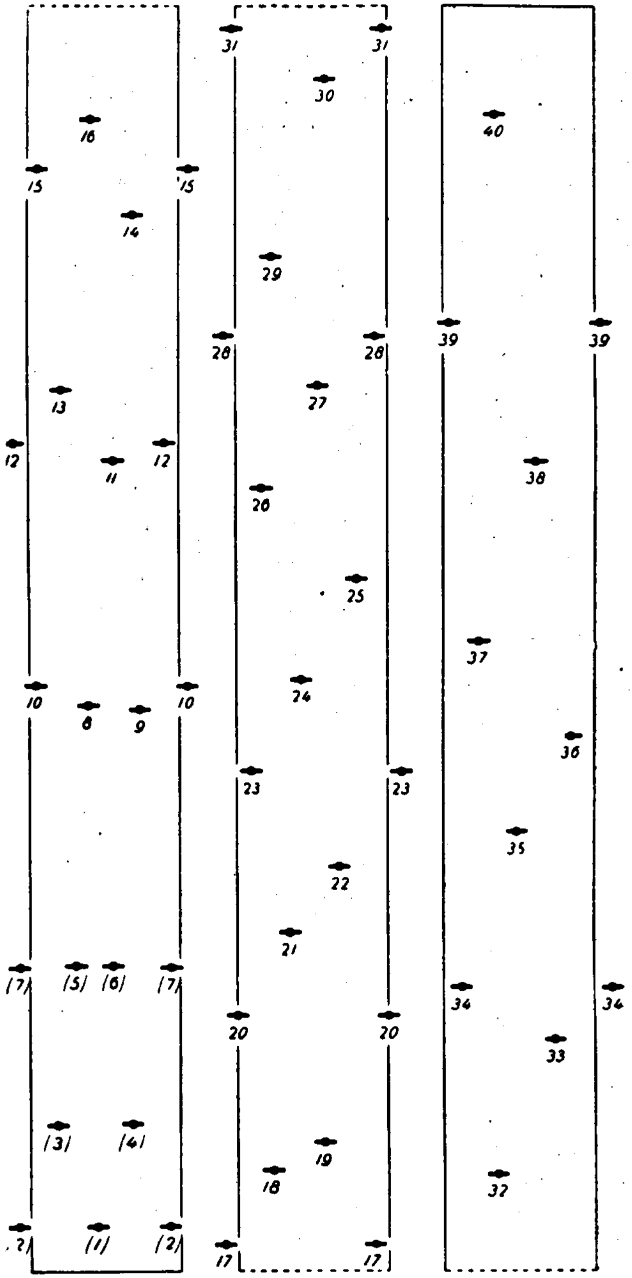
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Fig. 26—33. *Helianthus annuus*, unrolled surfaces of main stems of individual specimens, with indication of positions of cotyledons and foliage leaves by means of conventional figures.

In these figures the tapering stems have been drawn as if they were cylindrical, in order to facilitate the representation of the spatial relations between nearly superposed insertions; this was attained by measuring all transverse distances and reducing them to the same scale by calculation. Heights of insertion true to scale in the original figures, reduced in the printed figures as indicated.

Leaves numbered according to conspicuous systems; numbers in brackets in lower stem region derived from spiral in higher region.

Fig. 26 specimen with system of the main series and some trimerous binding whorls, × ¼.

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and any specimen in which the terminal head did not develop sufficiently to allow this counting was discarded.

The great majority of the specimens (262) proved to have patterns of the main series throughout; in the floral region the 21, 55 or 144 parastichies were always homodromous and the 34 and 89 parastichies antidromous to the spiral in the foliage leaves.

In 46 specimens the system belonged to the first accessory series, the 29 and 76 parastichies being homodromous, the 47 and 123 antidromous. In 9 specimens the first jugate series was indicated by the numbers 42 and 110, running in the sense of the dimerous leaf parastichies and the numbers 26 and 68, running in the sense of the tetramerous leaf parastichies. Finally only two specimens gave proof of the occurrence of the second accessory series by displaying the flower parastichy numbers 23, 37, 60 or 97.

1. Specimens with a phyllotaxis of the main series.

The usual condition in these specimens is the formation of a varying number of dimerous binding whorls of the same kind as in so many Dicotyledons; traces of the original spiral are only to be observed in the higher dissolving whorls. In these the lower partners of the pairs are arranged in the usual way according to an antidromous ¼ spiral.

The first visible deviation from pure decussation is either the convergence of two leaves, or in other specimens a level difference of two opposed leaves; in still other specimens both phenomena are combined from the beginning.

In a minority of cases (± 20 specimens) trimerous binding wohrls were formed; rarely directly above the cotyledons, usually after one to three, rarely after four dimerous whorls of foliage leaves. Fig. 26 gives an instance.

The leaves 20—40 in it are clearly arranged in a normal dextrorse spiral; 5—19 in five trimerous whorls which are only clear cut in the lower whorls, but gradually dissolve higher up. When traced backward from leaves 20—40, the spiral is to be followed through the trimerous whorls, and the insertion levels all correspond to the spiral numbering, with only the slight exception that leaf 8 is placed a few mm above leaf 9.

The divergences between the "cyclure" of any whorl and the "cyclarch" of the next whorl is clearly about 180° (10—11; 13—14; 16—17) as might be expected after what has been said in § 2.

Cases of the same kind were met with in sufficient number, so that the reliability of the facts is fully established. The most important complication was a connation of two leaves in the first trimerous whorl, being always those two leaves which lay above a single space of the dimerous whorl below. As connate or two-topped leaves are otherwise extremely rare (I only once observed them beyond the transition place in heteromerous whorl formation, namely in a specimen with a wholly irregular phyllotaxis and a dichotomy of the main stem) this connation no doubt is due to the crowding together of these two leaves under the influence of the adaptation to alternation (cf. SCHOUTE 51, p. 675). The figures 28 and 29 below illustrate similar occurrences in systems from other series.

Tetramerous whorls in plants with a system of the main series are rare; I only once observed two such whorls in a single specimen, illustrated in fig. 27. Above the two tetramerous whorls two trimerous whorls were formed, showing the same solution as those of fig. 26.

2. Specimens with a phyllotaxis of the first accessory series.

In these specimens the higher foliage leaves invariably showed a system $3 + 4$. On being traced downward this system proved to extend over a region of variable length.

In several specimens the system suddenly changed downward into a $2 + 3$ system of the main series; as the ternary parastichies in both systems were the same, running undisturbedly from the lower into the higher system, the genetic spirals in both systems were antidromous, making a sharp turn at the insertion of one individual leaf.

In other specimens the $3 + 4$ system had made its appearance earlier, so as to be present already in the binding whorl region. In the dissolving whorls of these specimens the opportunity needed for studying the binding is this anomalous series was realized; in the still lower perfect whorls no investigation was

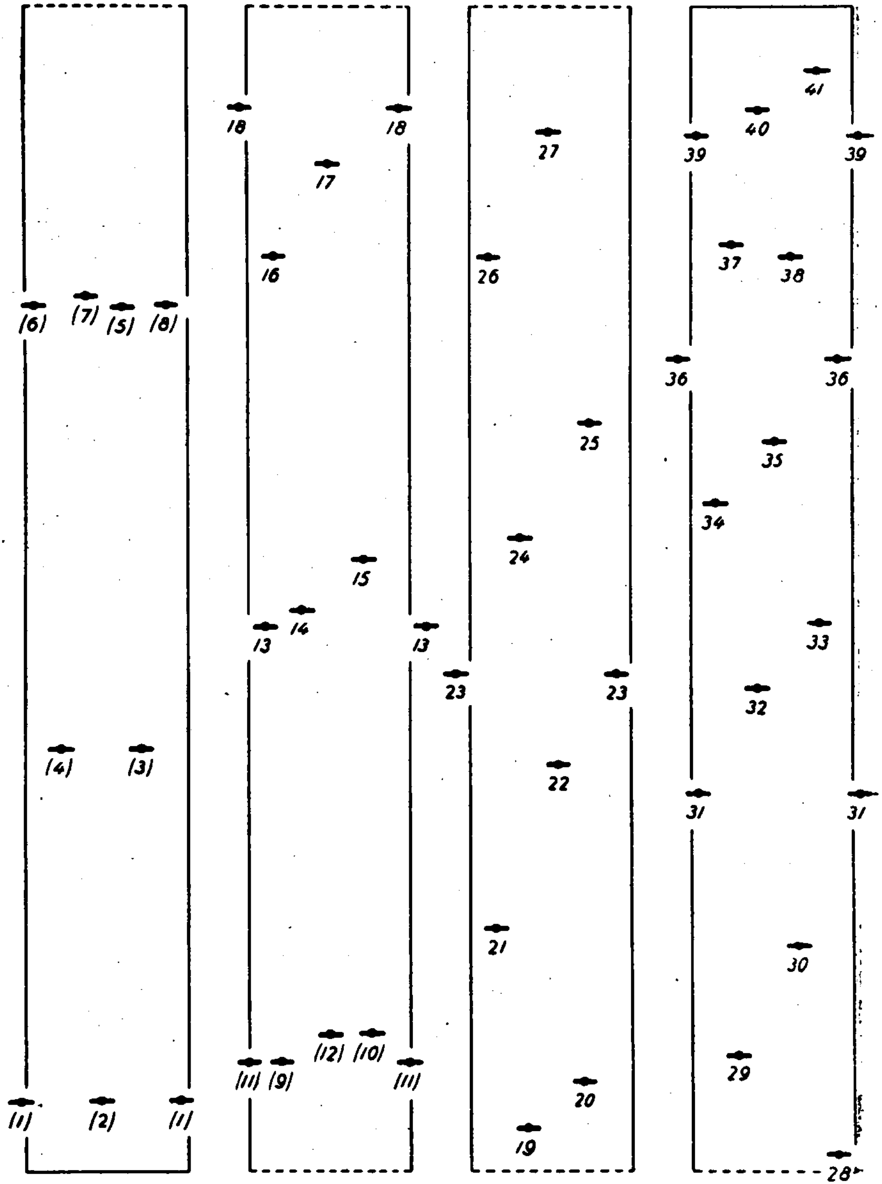

Fig. 27, see fig. 26. Phyllotaxis of main series and some tetramerous binding whorls, × ¼.

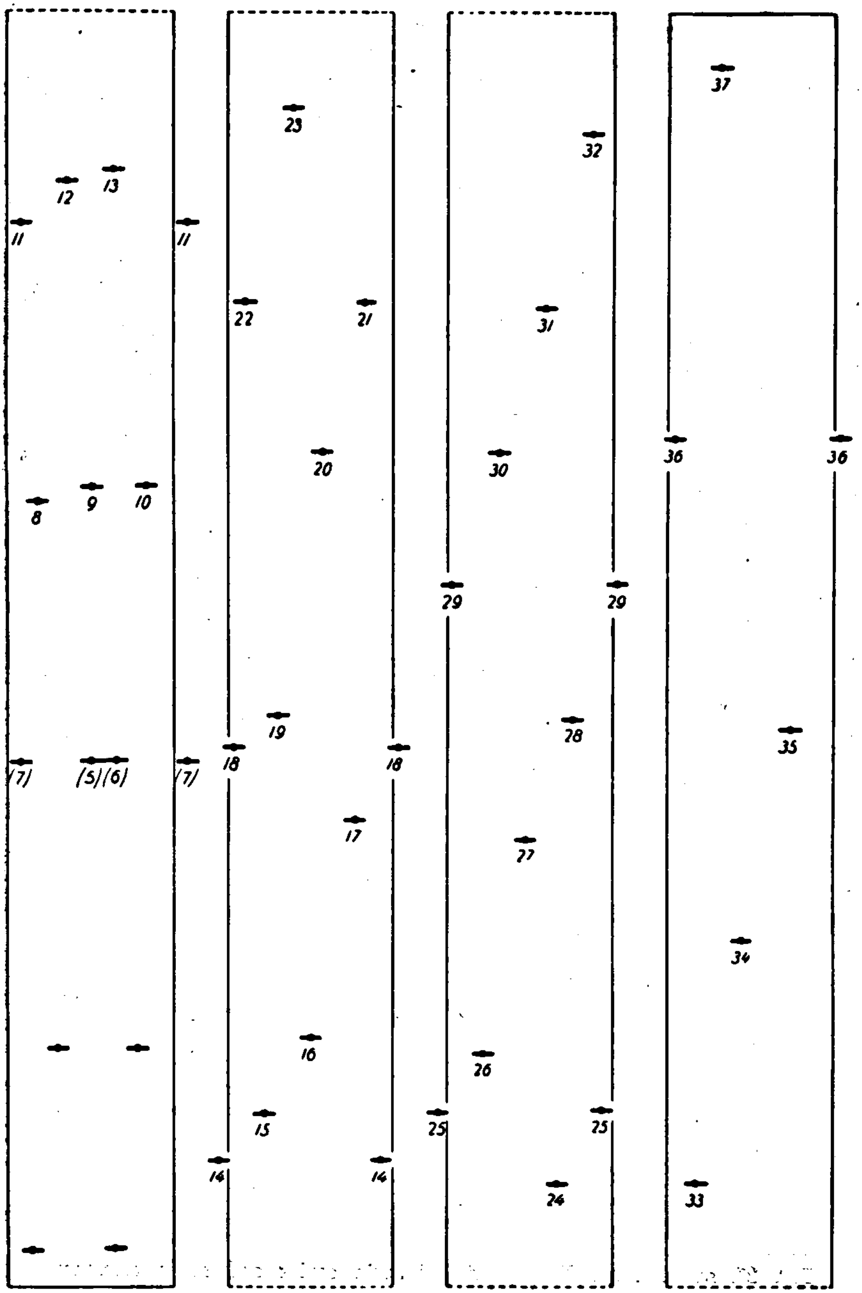

Fig. 28, see fig. 26. Phyllotaxis of first accessory series and some trimerous binding whorls, × ¼.

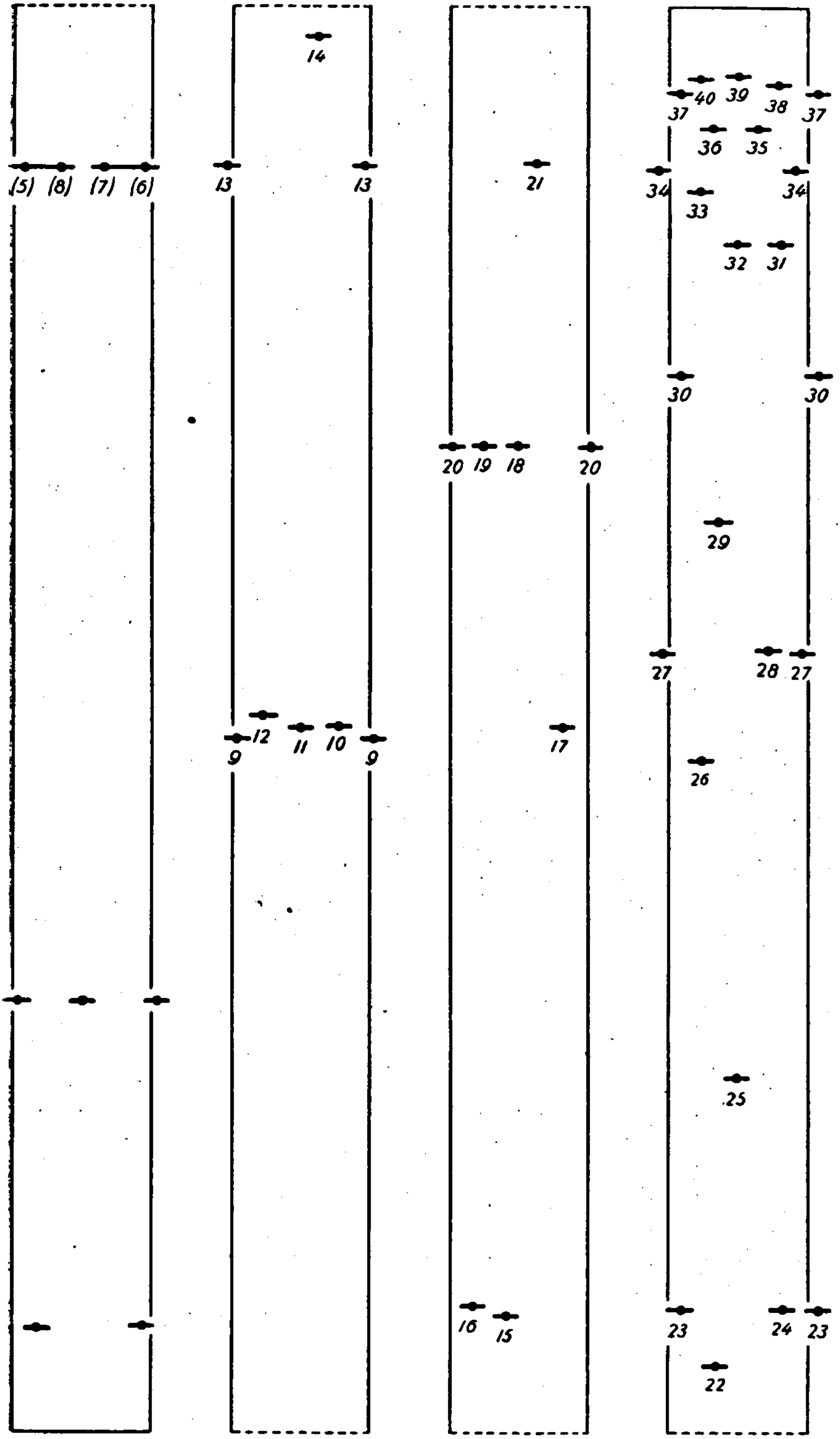

Fig. 29, see fig. 26. Phyllotaxis of first accessory series and some tetramerous binding whorls, × $^3/_5$.

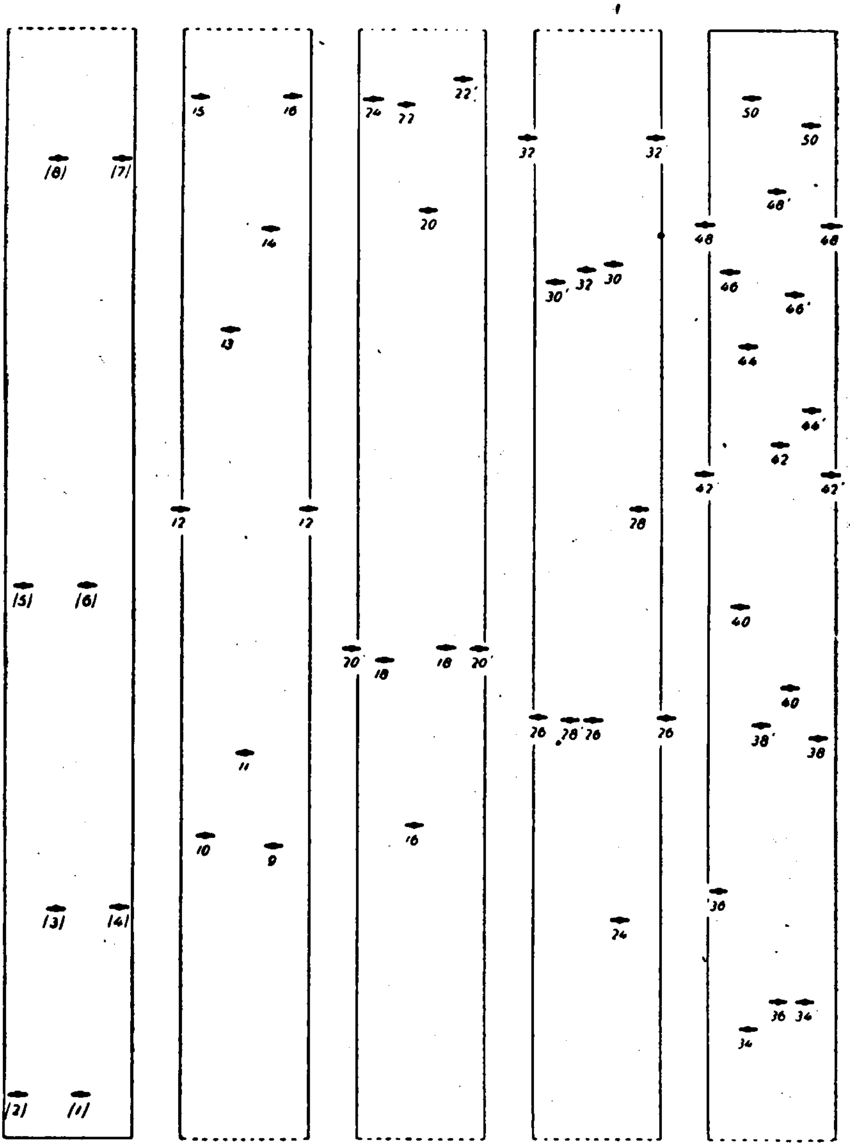

Fig. 30, see fig. 26. Phyllotaxis of first jugate series, × $^1/_5$.

possible for lack of criteria.

Yet it is almost certain that in all cases the initial system of the stem was one of the main series, as the cotyledons, and usually the lower leaves, were arranged in dimerous whorls, the formation of which is highly improbable if not impossible in the first accessory series; see § 2.

At any rate all whorls in such regions where the system was clearly 3 + 4 were either trimerous or tetramerous, the former being by far the most frequent.

Fig. 28 gives instances of the trimerous whorls. Two decussate whorls without any traces of the original spiral are followed by a trimerous whorl with two connate leaves in the usual arrangement above one space of the second whorl; the leaves 8—19 form four trimerous whorls with a progressive degree of solution.

In these whorls it is clear that the divergence between „cyclure" and „cyclarch" is 60° every time; from this observation in itself it might have been predicted that the subsequent stem regions should have systems of the first accessory series, with a dextrorse genetic spiral.

Our next figure 29 pictures another specimen, with tetramerous whorls. Here again two decussate whorls are formed first; the third whorl has two pairs of connate leaves, above the spaces of the second whorl.

The whorls 9-12 and 13-16 clearly are dissolved, and the fact that leaf 13 lies above the space between 9 and 10 points out a sinistrorse 3+4 spiral, in which the divergences have been changed into 90°, 90°, 90°, 135°. The leaves 17-24 form two further but rather indistinct whorls; 25-40 are almost spiral, but for some coherence between the whorl members (27 and 28; 31 and 32, 35 and 36, 39 and 40).

3. Specimens with a phyllotaxis of the first jugate series.

As expounded in § 2 the formation of dimerous binding whorls in this series does not require any metatopies, dimerous whorls being already realized in the system.

So on finding that the basal region of a specimen with this kind of phyllotaxis bears decussate leaves, it is impossible to tell whether the region is really a system of the main series in which binding whorls have been formed as elsewhere, or whether it is part of a jugate system.

However, in at least one of the nine observed specimens there was evidence that the former alternative was present; this specimen is represented in fig. 30.

As we see between the four basal dimerous whorls and the

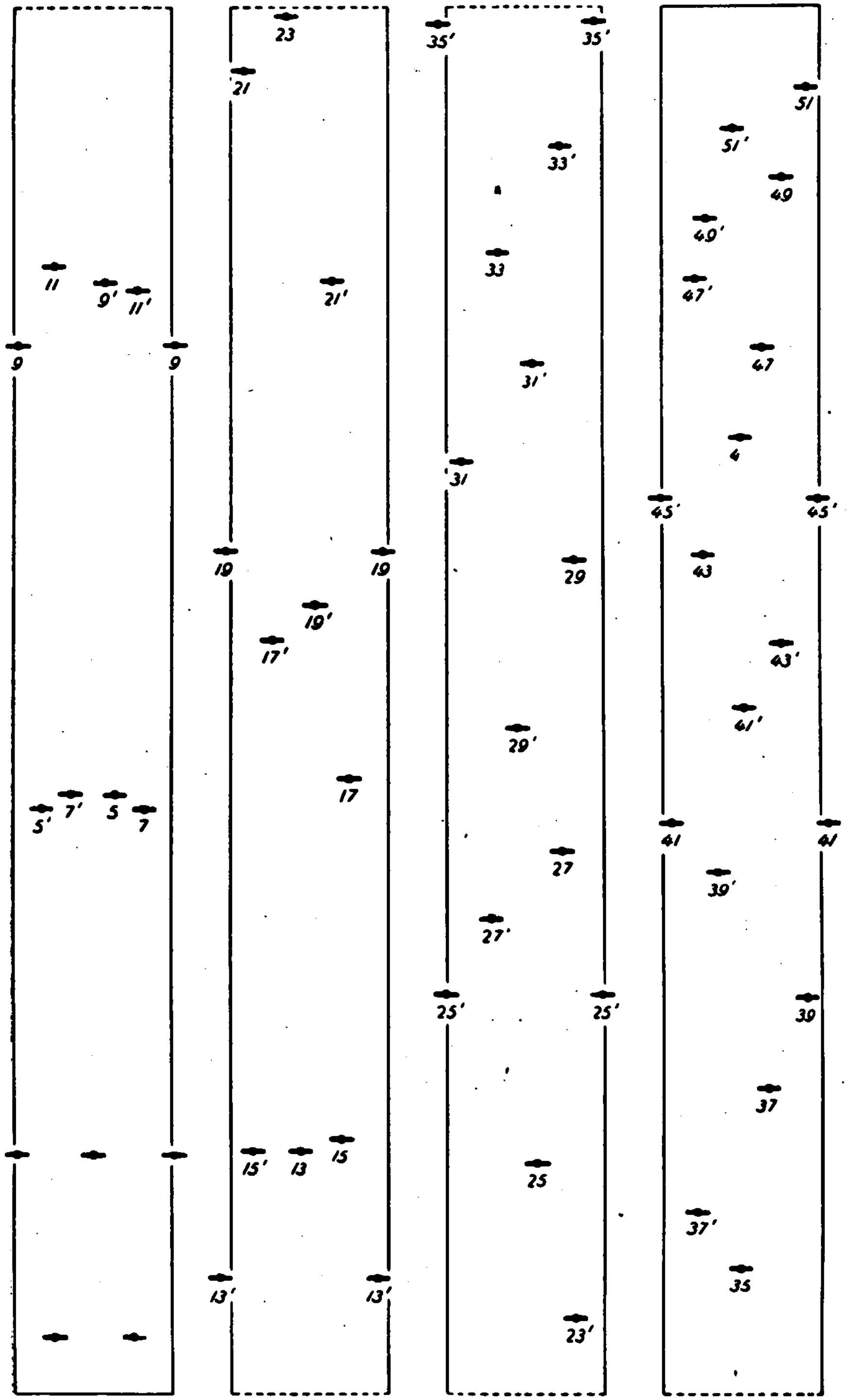
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Fig. 31, see fig. 26. Phyllotaxis of first jugate series and some tetramerous binding whorls, × ¼.

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higher jugate region an intermediate region is intercalated the arrangement in which is not so directly evident. The higher leaves have been numbered according to the jugate system, the leaves of a pair bearing the same number and those constituting one of the binary parastichies being distinguished by a dash. This has been continued in the downward direction as far as 16 and 16'; the lower leaves have been numbered as in a system of the main series.

In details the chosen numbering might have been varied here and there, but no numbering can change the fact that between the basal whorls and the higher jugate region an odd number of leaves is present (9-15 after our numbering) so that the decussate region and the jugate region can never belong to the same system.

Binding whorls other than dimerous whorls were poorly represented in my material; only a few tetramerous whorls were observed, being indistinct in some specimens and fairly well developed in one single specimen (fig 31). Here the leaves 5', 7', 5, 7 and 9, 11, 9', 11' were united into fairly regular whorls, 13'—19' into two dissolving whorls. In the latter the jugate system with two dextrorse and two sinistrorse parastichies is already fully established; the same system reigns higher up and the corresponding 68 s and 100 d parastichies could be counted in the flowers. The poor material did not give any opportunity for an investigation of the mode of whorl solution.

In both figures the reader will however remark that above the binding whorl region fragments of tetramerous whorls occur, and the same was observed in most of the other specimens.

In fig. 30 we find a regular repetition of three leaves at about the same level: 18, 20', 18'; 22', 24, 22; 26, 28', 26'; 30', 32, 30; 34, 36', 34' and 38', 40, 38, all in the position of three members of a tetramerous whorl. The fourth member in all cases is found to be shifted in the apical direction.

In fig. 31 we have in the same way three leaves keeping together: 15', 13, 15; 17', 19', 19; 23', 21, 23; 27, 25', 27', but here the leaves 13', 17, 21', 25 wanting in the tetramerous whorls are all shifted in the basal direction. As in both cases the shifted leaves form together one of the quaternary parastichies, we may also say that one of these parastichies has been shifted as a whole, in this region of the stem.

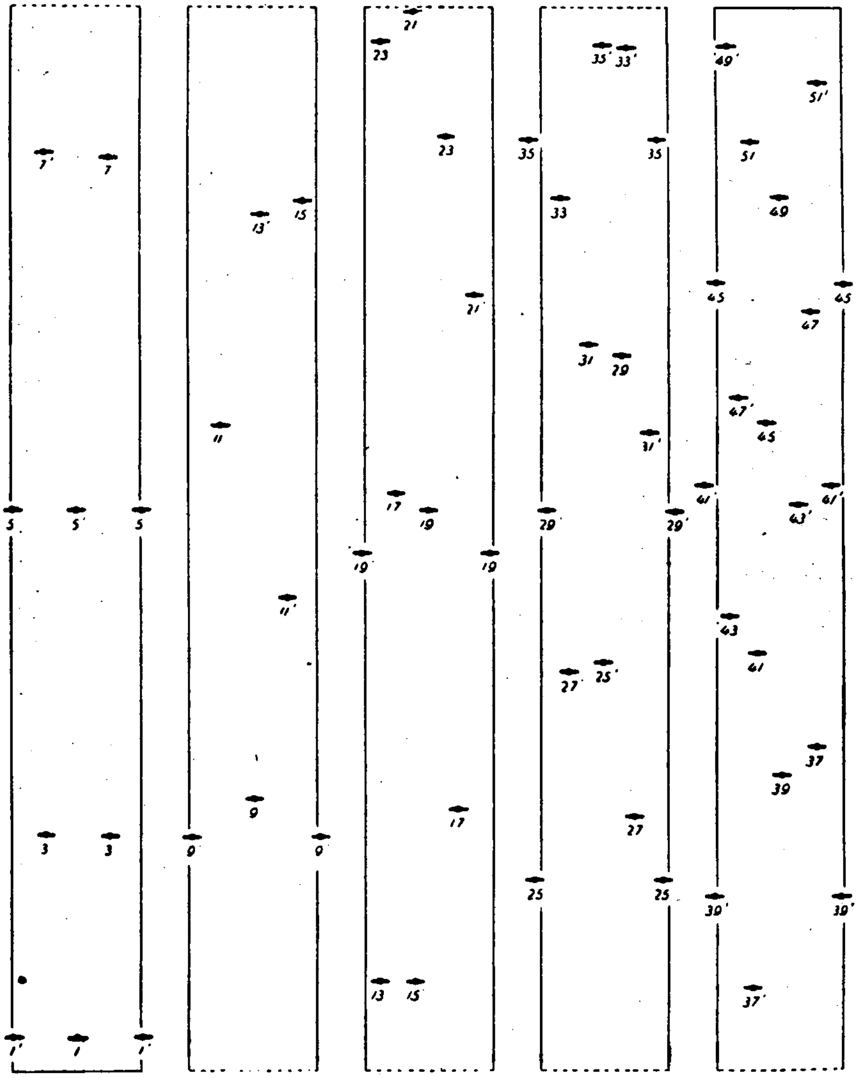

Fig. 32, see fig. 26. Phyllotaxis of first jugate series, × 1/5.

Yet it remains curious that in a region where the binding usually fails, three leaves keep together, as seems to be the case here; a possible explanation may be proposed.

The binding factors connecting the leaves in the lower stem region and dying away in the middle region, it is not impossible that their disappearance may begin with a shrinking of their radius of action, so that they can only connect leaves at unusually small distances.

Now in the jugate system all horizontal distances are exactly half as great as those in a system of the main series, so that a binding in unusually high stem regions is not improbable.

In one specimen a variation of the same condition was found, in the coherence of only two leaves, repeated in the same way four leaves higher up (fig. 32). Thus we see 23, 21; 27' 25'; 31, 29; 35', 33'; 39, 37; 43', 41' and 47, 45 keep together and the remaining leaves between these pairs keep together in the same way, though not so strikingly.

This may be due to a shift of two adjoining quaternary parastichies, and here too the leaves of the pairs may have kept together under the influence of binding.

4. Specimens with a phyllotaxis of the second accessory series.

One of the two specimens of this group showed rather indistinct, the other specimen well developed tetramerous whorls (fig. 33); the other probable form of whorls, those with five members, was not observed.

In the figure we see that after two decussate whorls one regular and four dissolving tetramerous whorls follow. The latter, comprising the leaves 9—28, clearly reveal a dextrorse $4+5$ spiral, and the successive divergences in this spiral are changed into 90°, 90°, 90°, 45°, so that leaf 14 lies above the space between 9 and 10, etc.

The same spiral is regularly continued in the region of the leaves 29—58; the involucral bracts showed the parastichies 9 s and 14 d and in the badly developed flower head 157 sinistrorse parastichies could be counted, 157 being a number of the series.

Summarizing our observations on *Helianthus annuus* we may say that the binding whorls are formed according to the same principles as in all other Dicotyledons, and that in stems with original systems of anomalous phyllotactical series the whorls are such as might be theoretically expected beforehand. It goes without saying that such a result is a confirmation of our views.

Finally we may point out the curious fact that in all three

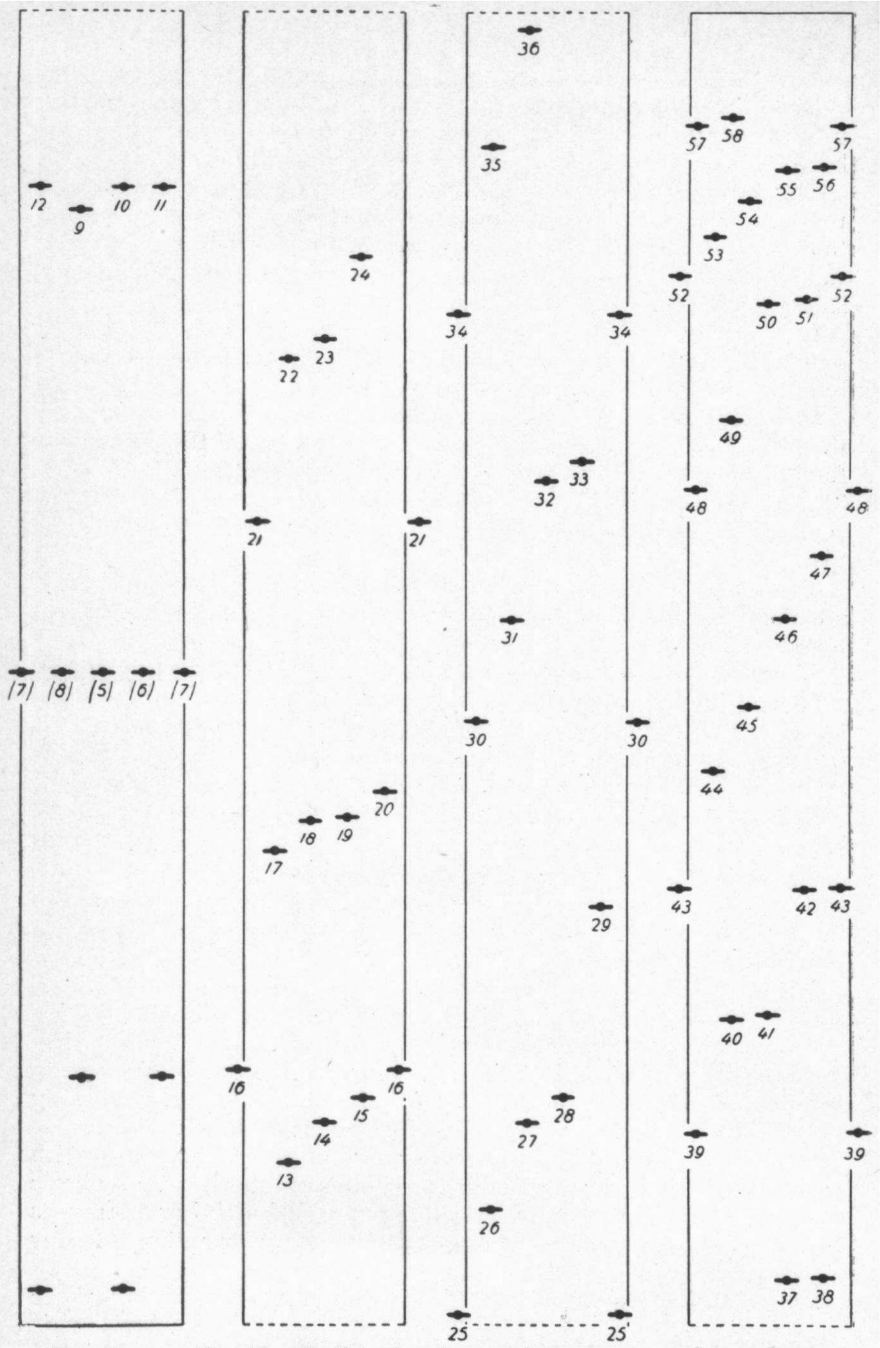

Fig. 33, see fig. 26. Phyllotaxis of second accessory series and some tetramerous binding whorls, × ¼.

spiral series two forms of whorls prevail, the lower one being more frequent than the higher one. This proves that for the establishment of a binding between two leaves a certain difference of insertion level is a more serious impediment than a transverse distance of the same measure.

CHAPTER 4. EXPLANATIONS FROM LITERATURE OF THE ORIGIN OF RADIAL BINDING WHORLS.

This chapter will contain a review and a discussion of the principal explanations for the origin of radial binding whorls given in literature by previous authors.

§ 25. Explanations of the origin of the whorled leaf arrangement.

1. Explanations by the principle of rhythm.

Some authors have enounced as their opinion that radial whorls are due to the property of the plant to produce its leaves with an oscillating value of the divergence angle.

When this angle is alternately 180° and 90°, or when two angles of 120° are succeeded by one of 180°, we only have to add a rhythmic growth and condensation of the successive internodes to obtain regularly alternating dimerous or trimerous whorls.

This was the view held by Schimper and Braun (5, p. 167) for all radial whorls. As is well known they clothed it in the form of a fixed divergence with a negative or positive addition at the transition between two whorls; this prosenthesis has especially given rise to a good deal of criticism.

And indeed we cannot see an explanation in this mode of describing the facts; for an explanation we should have wanted arguments for the necessity of these rhythmic phenomena.

Yet the description in itself is not only correct, but the occurrence of the numerous phenomena described above as deficiencies of the horizontal and longitudinal metatopies fits in very well with this view, as it requires only a somewhat less pronounced rhythm. Moreover the accompanying phenomena of the discontinued whorls and those of the bud spirals all fit in very well, and we may be sure it was especially these latter phenomena which brought Schimper and Braun to their views on the topic, and we may add that it was those botanists who did not know about these phenomena who were the first to take offence at their prosenthesis.

A similar description, but this time wrong in itself, has been given by DELPINO (16, p. 248) who believed that decussation can arise in three different ways: by a rhythmic development of the internodia in a spiral phyllotaxis, or by a doubling of one of the three ternary parastichies or an abortion of one of the quinary parastichies in the same spiral phyllotaxis.

The first process gives rise to the spurious decussation which only occurs in transitional regions as an unstable equilibrium (p. 239), the second and third are the cause of the regular decussation where the first leaves of successive pairs are arranged in a zigzag. This form is realized in the *Caryophyllaceae* (sic!), in *Eucalyptus* and many other plants (p. 240, 242, 247).

WYDLER (84, col. 820) in his last paper, published the day after his death, pointed out that the two forms of decussation distinguished by DELPINO did not correspond to the two actual forms and a perusal of DELPINO's argumentations indeed shows that his suppositions are nothing but inventions without any foundation.

2. Explanation as true whorls.

Several authors are inclined to take the radial whorls of Dicotyledons as true whorls, as an original and genuine phyllotaxis therefore.

For arguments against this view I may refer to my paper on false whorls (51, p. 678); moreover the deficiencies of the metatopies described above would all remain unexplained if the whorls were true whorls. So this view is not to be accepted, though it has been held amongst others by the BRAVAIS brothers (11, p. 16), HOFMEISTER (28, p. 440), SCHWENDENER (54, p. 82), WEISSE (64, p. 293), CHURCH (14, p. 142), GOEBEL (25, p. 197), the SNOWS (55, p. 91) and TROLL (60, p. 409).

For some of these authors the whorl is due to a tendency to perfect radial symmetry (CHURCH, GOEBEL, TROLL), for others it is a haphazard result of the junction of new leaves with older ones (HOFMEISTER, SCHWENDENER, WEISSE, SNOW and SNOW).

For both groups the deficiency phenomena described above present a serious difficulty in the way of understanding, as remarked earlier. The difficulty may be partly overcome by the authors of the former group: once a nature philosophy principle such as symmetry is accepted as an explanation, another principle of the same description, the spirotrophy, may be made responsible for some of the phenomena in question (GOEBEL 25, p. 199) giving a seeming explanation; other phenomena however remain unexplained, as for instance the fact that a phyllotactical spiral in discontinued whorls is always antidromous to a bud spiral in the decussate region.

In a somewhat different way the difficulty is met by TROLL (60, p. 418) who after having discussed my preliminary paper on radial decussation (48) remarks that the decussation of the *Caryophyllaceae* probably represents a beginning of a transmutation of true decussation into a spiral arangement.

This view is opposed to my explanation by means of metatopy, about which the author remarks: „Zunächst ist nicht einzusehen, warum die Annahme von Verschiebungen, vor allem lateralen Metatopien, die stark an das erinnern, was man früher als „Prosenthese" bezeichnet hat, verständlicher sein soll als die einer spirodromen Förderung, die durch zahlreiche Vorkommnisse im niederen und höheren Pflanzenreich doch wahrlich genugsam und so vielfach belegt ist, dass es heute mehr denn zu GOETHES Zeiten Sinn hat von einer „Spiraltendenz der Vegetation" zu sprechen. Belege dafür liefert die ganze folgende Darstellung der zerstreuten Blattanordnung bei den Monokotylen, Dikotylen und Pteridophyten". (60, p. 418).

In fact, if we might assume true whorls in the lower shoot region, due to a perfect symmetry, and a spiral tendency in the higher shoot regions, the phenomena described above as deficiencies of metatopy might be placed among the consequences of such a change of tendency.

Our chief objection to this conception is however that it does not afford an explanation at all, as being of an idealistic kind, without a physiological background. The fact of an endless repetition of a spiral construction in nature no more gives any insight into its causes than the repeated fall of free bodies explains to us why gravity exists;it only proves that the causes for a spiral arrangement must be wide-spread.

The explanation by means of metatopies on the other hand is essentially of a physiological character, notwithstanding its numerous imperfections through want of knowledge of the facts; it opens the way for further investigations.

Moreover the required metatopies are not purely hypothetical; those plants in which the primordia are convergent and the adult leaves opposed, prove their existence, and so do the symmetrically bending leaf-traces of *Antirrhinum,* by showing us the results of such shifts. In the third place the phenomena of biastrepsis, due to an abnormal order of the normal binding processes, fit in perfectly with the views proposed here, and would be unexplained in TROLL's sphere of ideas, requiring the assumption of a new ideal principle, with the curious peculiarity that it would be present in all plants with binding whorls, but would nearly always remain inactive, except in rare teratological cases.

So the choice between the two points of view to my opinion is not difficult.

In the case of the authors of the second group, who take the whorled condition as a result of junction phenomena, the great objection is the regular occurrence of whorled systems in so many species (see 51, p. 672). In many plants the decussation has been supposed to be explained as an original phyllotactical system built up on the opposed cotyledons or the opposed prophylls. But as soon as we realize that in most of these plants the decussate region only varies with trimerous whorls, never with spiral systems, it becomes clear that such a condition is not to be reconciled with a haphazard origin of the whorls.

Accordingly attempts to explain the transition of the supposed true whorls to spiral arrangements as junction phenomena are rare in literature; one of them made by WEISSE in 1894 may be discussed here.

Having observed that in dimerous and especially in polymerous whorls the tangential extension of the leaf insertion is relatively narrow, narrower than is usual in scattered leaves, WEISSE supposes that the origin of whorls is necessitated by the form of the young primordia (64, p. 293).

It needs however no discussion that a relatively narrow insertion is only one of the requirements for whorled phyllotaxis, but can never be one of its causes.

No explanations on the basis of a junction theory seem to have been given by any author of the convergences in the leaf pairs or of any other phenomenon of deficiency of metatopy; and it would indeed be difficult to give one. When we observe for instance that the transition of decussation to spiral arrangement may begin with convergences in the pairs only, or by level differences only, or by both at once, this is not to be reconciled with a junction theory, as any level difference in a true whorl must cause a convergence in the next one, and reversely.

It is only for the occurrence of the bud spirals that we find some explanations of this kind, given by HOFMEISTER and by SCHWENDENER.

HOFMEISTER (28, p. 500) writes that in plants with radial dimerous whorls all primordia first extend farther to one side, either to their right or to their left, all to the same side in the same shoot; when they grow older, the other side extends too.

Now if one of two opposed leaves is somewhat older than the other, it extends to both sides at the moment in which the younger leaf only extends to one side. So the spaces for the next whorl are unequal, and the leaves of this whorl will be of unequal age too.

According to HOFMEISTER the successively older leaves are in such a way placed in a ¼ spiral, and as their axillary buds are furthered, the bud spiral is the outcome.

Against this explanation we have not only to object that the one-sided development of the young leaves is not confirmed by any observation, but the whole theory is erroneous; any construction will make clear that when we pursue the reasoning we find that the third whorl will consist of two leaves of the same age which are more or less opposed; a ¼ spiral of the older leaves does not ensue. Moreover we find that the third leaf is nearer to the second than to the first, which is contrary to all observation.

SCHWENDENER, recognizing that HOFMEISTER's theory is not supported by any facts, gives another and logically more consistent theory (54, p. 84) based on the assumption of a shift of one of the binary parastichies in its own direction. Such a shift really might be explained by junction phenomena only (comp. 46, p. 237, fig. 25) and it would entail age differences of the leaves in the pairs in the required succession. So on a former occasion (46) I accepted this view. After having studied the phenomena however I had to change my opinion, as the regular occurrence of the bud spirals is against it, and especially as such a shift would never be able to convert the orthostichies into winding spirals.

Yet as described in § 9 such winding orthostichies are not rare. HOFMEISTER mentions the fact, but SCHWENDENER writes of it that he could not confirm it and that he considers it to be "theoretisch unmotivirt" (54, p. 85).

The last paper to be discussed here is one by M. SNOW and R. SNOW (55), in which the authors describe a transition from decussation to spiral phyllotaxis in *Epilobium hirsutum* and in which they claim to prove that only junction phenomena are the cause of this transition.

The starting point of the authors is the idea, defended earlier by HOFMEISTER, SCHWENDENER and VAN ITERSON, that it is not the leaf centre which is determined first, but that it is the junction of the outline of its insertion with lower insertions which is responsible for the determination of the position of the new leaf.

For this thesis they give an experimental basis by making a radial split, running in the diagonal direction between the four leaf orthostichies, in growing apices of *E. hirsutum*. The wounded apices in regenerating develop a new apex, occasionally two; the phyllotaxis of these new apices is partly developed on the base afforded by the older leaves and partly on the wound margin.

In these regenerated apices the authors observe that the new leaves are always to be found in those places left free by the edges of the older leaves; consequently they conclude that the position of the new leaves has been determined by these edges.

In my opinion this conclusion is only due to a confusion between results and causes; all leaves whether in normal or in abnormal situations during their young stages extend their insertion, and, within certain limits, they do so up to the available space. Hence we observe many asymmetrical leaf insertions in the regeneration products, and moreover several fused leaves, furnishing a clear proof of the union between two extending edges.

In some cases a new leaf was observed to be formed above the SW-angle between the two lower leaves, instead of above the LW-angle. This is explained by the authors by the fact that the two lower leaves having extended asymmetrically towards the LW-side, the largest gap between the edges was actually that on the SW-side.

As in those cases the LW-side was situated closely above the wound the real explanation may be that by the wound reactions the gap on the LW-side was less appropriate for the formation of the next leaf, and once the next leaf was formed on the SW-side, the edges of the lower leaves, finding an unusually large space on the LW-side, grew out asymmetrically.

The authors further claim to have converted the apices with a normal decussate phyllotaxis by their operations into apices with a spiral phyllotaxis (55, p. 91). This conclusion does not seem warranted on the following arguments.

Without any treatment the operated apices would have lost their binding and would have become spiral in a very short time [1]. So it is very natural when some of the new apices were quite or nearly decussate (6 specimens), others were regularly

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[1] The buds of inflorescences are formed according to the authors at the very end of May. So the binding at this time disappears, as the observation of the adult condition shows us that the whorl formation disappears in the region of the lateral inflorescences. The examined shoots were dug up and planted in April or early May, allowed to recover for a week, operated upon, and then pickled after 14 to 20 days, sometimes even later.

spiral (10 specimens) and the majority showed an intermediate condition, with oscillatingly large and small divergences, either in the lower part of the regenerated apex only (7 specimens) or all over the new apex (13 specimens). In the latter group the first divergence ranged between 141° and 185°, the second, third and fourth between 92° and 124°, 142° and 175°, 110° and 140°.

The SNOWS admit that these cases "may be considered in a sense intermediate" between spiral and decussate (p. 78); according to our view the explanation is that the action of the binding factors had been present in them, but in a weakened condition.

In particular a small group of three specimens is remarkable in this respect: in these apices the successive angles between the first five leaves were: 148°—161°, 123°—130°, 125°—131°, 151°—156°, 123°—136°. Thus we see after the first large angle two small ones follow, after which the normal oscillation is restored.

No explanation for these cases is given; we may be sure however that they are due to a first binding of the leaves 1 and 2, and then of 4 and 5, leaf 3 being left alone. Such an irregularity may easily have been induced in some way or other in these seriously ill-treated apices (1).

3. Derivation of whorled from spiral phyllotaxis in a phylogenetic way.

A third view is held by ZIMMERMANN, namely that the whorled condition in the Cormophytes is due to some phylogenetic changes in the hereditary phyllotaxis which originally was a spiral one (86, p. 319).

In itself the ontogenetic elaboration of binding whorls, by changes in a spiral system under the influence of special binding factors, must have its phylogenetic counterpart in the formation, in the course of evolution, of the hereditary factors for such

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(1) In a quite recent paper the same authors describe new cases of transition from decussation to spiral phyllotaxis in *Epilobium hirsutum* (56), this time not the consequence of an operation, but being conditioned by application of auxin to the shoot apex above the youngest primordia.

Here the subsequent change in phyllotaxis is explained (p. 11) as a consequence of a lateral shift of one of the first newly formed leaves; an explanation which is not very satisfactory as this lateral shift is the beginning of the changed phyllotaxis itself, and has itself to be explained.

According to the views of the present author the whole case is rather simple: the binding factors which at least in some of the shoots may have been about to be inactivated, may have been suddenly inactivated by the stimulation emanating from the auxin.

a binding. So the view of ZIMMERMANN might correspond to the view given in the present paper; a closer examination however soon reveals a number of important differences.

The changes in the hereditary phyllotaxis are according to ZIMMERMANN threefold: a reduction of the internodes between the whorl members, an equalization of the angles between the whorl members and a specialization of the plastics of the different whorls.

The latter change will not be discussed here, as not pertaining to whorl formation but only to a further differentiation, facilitated by a previous whorl formation.

Concerning the first and the second change we may remark that ZIMMERMAN's view would only have a biological meaning for the case where the internode reduction and the equalization of the angles were due to the action of special hereditary factors, as ZIMMERMANN himself expressly states (p. 262).

Now as neither the internode nor the divergence is a separate biological unit, being both as I remarked earlier (51, p. 672) nothing but casual results of the spatial relations between the leaves, such a regulation by special genes is very improbable, and by a consideration of the variation of both in analogous parts of the same plant, we come to the conviction that it does not exist.

4. Miscellaneous remarks.

Some authors, without giving a theoretical explanation of the origin of the whorls considered here as binding whorls, have given views or remarks on the phenomena in question which may be discussed here.

In 1874 VAN TIEGHEM distinguished between two categories of decussate or whorled systems (58), the one being characterized by a simultaneous origin and an exact equivalence of the whorl members, the other by successive, more or less different leaves in the whorl.

The former category "being well-known" is not discussed; for the latter the *Caryophyllaceae* and *Rubiaceae* are quoted. After what has been said in our previous chapters it will be clear that this view which has already been refuted by AL. BRAUN (8), is wrong.

On the occasion of his study of the phyllotaxis of *Phyllactis rigida* BENOIST came to the conclusion that the usual connation of the leaves of this species into two spirals demonstrates that the theory of SCHIMPER and BRAUN of the single genetic spiral is to be abandoned in favour of that of the BRAVAIS brothers about a single spiral in some plants and more spirals in others. (1, p. 491, 2, p. 563).

As *Phyllactis rigida* is not decussate at all (cf. § 12), Benoist's conclusion which already on other grounds is not to be accepted, loses its whole basis.

Finally we have to quote here the enouncement by Zimmermann (86, p. 264, 267, 287) that in decussate shoots a period of eight leaves is present, forming a unit, and similarly in trimerous whorls a period of 18 leaves, and Zimmermann adds that Al. Braun was already aware of this fact.

This statement is quite correct, if we realize that the described "unit" of eight leaves has no biological value, but is only a mathematical abstraction.

From the fact that above any leaf the ninth leaf is situated in an analogous position, it does not follow that there are biological units with a marked beginning and ending; in reality the whorl is the only unit, containing all the elements of the whole system.

§ 26. Explanations of the origin of the bud spirals.

For Schimper and Braun the bud spirals were due to the differences in age of the whorl members, according to the original spiral; for Hofmeister and Schwendener the same age differences were the cause, the differences themselves not being the outcome of a spiral origin, but being junction phenomena.

For those authors who take symmetry as a ruling power, the bud spirals are direct consequences of the spirotrophy, the furthered buds being subtended by furthered leaves.

All these views are directly refuted by the fact that in some natural orders the advanced bud is subtended by the youngest leaf, and the view given in § 10 of the present paper therefore must be preferred.

Quite a different view has been expressed by Raciborski (41, p. 4); it amounts to the assumption of a more or less independent cladotaxis. As Raciborski puts it, the young primordia represent centres of vegetation, changing a certain zone of the vegetative cone into an area which attracts the nutritive substances.

Now we cannot deny that there may be mutual relations, according to laws of their own, between the axillary buds; the cases of cladotaxis in Pteridophytes (61, p. 10) illustrate this clearly.

In whorled plants Raciborski mentions bud spirals with a divergence of ¼ (*Galium, Lasianthus, Cupressus*), of $^1/_3$ (*Cupressus*, in trimerous whorls), of ½ (*Cupressus*, small branches), of

$^2/_5$ (*Acacia verticillata*), of $^3/_8$ (*Casuarina sumatrana*).

Some of these cases (*Galium, Lasianthus, Casuarina*) may be explained along the lines followed in the present paper; *Acacia verticillata* is probably not whorled at all (Buscalioni and Catalano 12; Goebel 26, p. 277). The cases of *Cupressus* however require a different explanation from that given for Dicotyledons, and that by Raciborski deserves our full attention.

There is one important difference between *Cupressus* and the Dicotyledons; as Raciborski mentions, the intercalation of one or more sterile whorls does not interrupt but changes the branch spiral. So if in a $^1/_4$ bud spiral a sterile whorl intervenes it is not the fifth whorl but the sixth which has a bud in the same position as the first. This of course is full proof that it must be different factors which rule the bud distribution.

By my own observations I can fully confirm Raciborski statement, at least for the distichous branch arrangement, in *Libocedrus decurrens, Thuya gigantea* and *Th. occidentalis.*

In these three species the somewhat dorsiventral smaller branch systems are decussate with laterally compressed lateral leaf pairs and flat adpressed median pairs.

Branches are exclusively formed from the axils of some of the lateral leaves; in a leaf pair more than one branch is never formed and many lateral leaf pairs are wholly sterile.

As a rule the lateral branches alternate regularly, irrespective of the fact whether sterile pairs are intercalated or not. Exceptions are to be found in some cases in the last part of a shoot, where the lateral branches are more remote and where occasionally two lateral branches may be superposed, evidently on account of the large distance not having been bridged over by the cladotaxis. Moreover exceptions are always found at the shoot base, where, probably under the influence of the mother axis, a number of superposed branches is always found at the adaxial side of the shoot; compare fig .24 and 25 of Raciborski (41, p. 44).

As instances I may give the following data about two shoots of different order of *Thuya occidentalis.*

Shoot 1 (larger branch) node 1 sterile, node 3 branch at left, being in this case adaxially, 5 l, 7 l, 9 r, 11 l, 13 s, 15 r, 17 l, 19 s, 21 r, 23 s, 25 l, 27 s, 29 r, 31 s, 33 l, 35 s, 37 r, 39 s, 41 s, 43 l, 45 s, 47 s, 49 r, 51 s, 53 s, 55 l, 57 s, 59 s, 61 s.

Shoot 2 (higher up) 1 s, 3 r, 5 r, 7 r, 9 r, 11 r, 13 r, 15 s, 17 s, 19 s, 21 s.

Raciborski introduces for the case of the alternating branches the term monopodial fan, for that of the superposed branches monopodial sickle. The use of these terms is not to be recommended as the present arrangement is due to causes quite different from those in monochasia. Yet his description itself is quite correct and his conclusion about influences emanating from one developing bud to the higher buds has to be accepted.

In view of this result we might ask whether our explanation of the bud spiral in Dicotyledons has to be revised accordingly. As however in the latter cases the intercalation of a sterile whorl never influences the bud spiral which is continued as if the sterile leaf had been fertile, and as moreover the course of the bud spiral always corresponds to the course it should have according to the original spiral, there is no reason to do so.

CHAPTER 5. DORSIVENTRAL BINDING WHORLS IN GENERAL.

In the present paper those binding whorls will be called dorsiventral, where according to what has been written in § 4, the whorl organs on the different sides of the shoot have developed differently or have been subject to different shifts, under the influence of the different sets of morphogenetic forces on the sides of the shoot; these phenomena are exactly the same in dorsiventral shoots with whorled as in those with spiral phyllotaxis.

In literature several explanations have been given about the origin of such a dorsiventral differentiation.

The old view of **Hofmeister** that such a differentiation is a direct consequence of external forces, especially of gravity, is no longer accepted in our day. But when **Goebel** writes that it seems unquestionable that a stronger growth of any part is based on a better supply of nutritive substances (25, p. 213, 26, p. 301) or when **Boshart** writes that the size of any part is determined by the area alotted to it at the apex (3, p. 121), these views are not to be accepted either, or rather they have to be reversed.

Any organ in which a special kind of growth is induced by the morphogenetic forces, be it stronger or weaker or simply different from others, takes possession of as much and of such nutritive substances and of as much space as is required for its development, within the limits of what is possible in the case; and stronger leaves having stronger veins, are not larger on account of a better accomodation due to more conductive elements, but the outer as well as the inner complexity are both the consequences of the stronger growth induced by the morphogenetic forces.

Of course it is another question which lies outside the scope of the present paper, how the distribution of the sets of morphogenetic forces may be influenced by outside forces.

§ 27. Polymerous dorsiventral binding whorls.

In polymerous binding whorls of vegetative leaves dorsiventrality seems seldom to have taken much hold on the shoot organization; the best example known to me is that of some *Cuphea* spp. (*C. lysimachioides* and *C. spermacoce*) in which according to the description by KOEHNE (31) we have tri- and tetramerous leaf whorls with one single vegetative bud in every whorl, the other buds being flower buds. The vegetative branches all lie on the same side of the shoot and consequently are placed in a zigzag, in the trimerous whorls with 60° divergence (KOEHNE 32, p. 111).

In polymerous floral whorls as is well known dorsiventrality occurs often, and here it has led to far-reaching specializations and adaptations. As it is not certain however whether floral whorls are binding whorls, these cases for the time being lie outside the scope of the present paper.

§ 28. Dimerous dorsiventral binding whorls.

In dimerous binding whorls the influence of dorsiventrality is often strikingly elaborated and it may enter deeply into the organization of the shoot.

This influence in the present paper is taken to be superposed on or combined with the action of the binding factors, giving rise to additional shifts of leaves or buds and to different plastics of the differently placed organs. The validity of this conception may perhaps be checked by the facts to be described below.

By the dorsiventrality a number of phenomena may be brought about which may be combined in the same plant in any way. These phenomena will be dealt with here under separate headings.

1. Assumption of a fixed spatial relation between phyllotaxis and dorsiventrality plane.

It is a remarkable and wholly unexplained fact that a fixed relation between the dorsiventrality plane and the phyllotaxis may arise.

In plants with a weakly expressed dorsiventrality such a relation is not always present. In *Ruellia Makoyana* where the lateral shoots are isophyllous but a certain dorsiventrality arises through a definite orientation of the leaves towards the light direction, some shoots are orientated in such a way that the leaf pairs have median and lateral positions with respect to the dorsiventrality plane, in other shoots they are placed diagonally and in still others they may have any intermediate position.

In *Strobilanthes rotundifolia* the same differences of leaf pair position were observed, though a somewhat more pronounced dorsiventrality is present, as the under leaves are decidedly larger than the upper leaves. In a diagonally dorsiventral shoot we have therefore two rows of smaller upper and two of larger under leaves; in a shoot with transverse and median pairs the lateral pairs are isophyllous, the median pairs strongly anisophyllous, and in shoots with an intermediate condition the leaf sizes vary accordingly.

On the other hand in *Dipteracanthus squarrosus* which only has a slightly pronounced dorsiventrality and which is isophyllous, I never saw any shoot with other than a diagonal position of the leaf pairs.

In decussate plants with a well developed dorsiventrality a fixed relation always occurs, and here either the lateral and median position or the diagonal position is realized.

The former is the less frequent: it is to be observed in the *Cupressaceae*. In Dicotyledons it is rare; the only instances mentioned in literature as far as I know are the following.

The Bravais brothers (11, p. 20) and Wichura (67, p. 236) write that in *Justicia Adhatoda* the flowers in the lateral spikes occur in the axils of the lateral and anterior bracts, the posterior bracts being sterile.

Raciborski describes *Gmelina parviflora*, a Verbenacea, in which the horizontal and dorsiventral secondary and tertiary branches have lateral and isophyllous leaf pairs (41, p. 24, fig. 11), alternating with median and anisophyllous pairs, the leaves of the physiological under side being much larger.

Finally Raciborski observed in *Crossandra infundibuliformis* and *C. undulaeformis* sympodial shoots, each sympodium member bearing two pairs of decussate leaves and a terminal inflorescence. In any member the anterior leaf of the second pair being fertile and producing a new sympodium member, the successive inflorescences in the sympodium are superposed (41, p. 59).

In some dry branches of *C. unduliformis* received from Buitenzorg I could confirm the main results mentioned by Raciborski, though I could not determine whether the shoots were sympodial or not. It was however perfectly clear that all lateral leaf pairs of the complex were isophyllous, the median pairs anisophyllous, the leaf at the side of the inflorescence being much smaller. So whether the shoots are monopodial or whether they are sympodial, the dorsiventrality at any rate is of the same kind as in the former examples.

For the other relation, that with diagonally placed leaf pairs, it is not necessary to quote examples as it is the common condition in dorsiventral and decussate Dicotyledons.

When we now ask whether in shoots with a well developed dorsiventrality the usual relation between decussation and dorsiventrality is absolutely fixed, our answer must be in the negative. In exceptional cases we may observe that there is some irregularity, some shift of the orthostichies, so that for instance instead of the third and fifth leaf pair lying above the first it is the fourth pair which is superposed to the first, the second and third pair assuming intermediate positions.

Cases of this kind were observed in *Herniaria glabra,* where

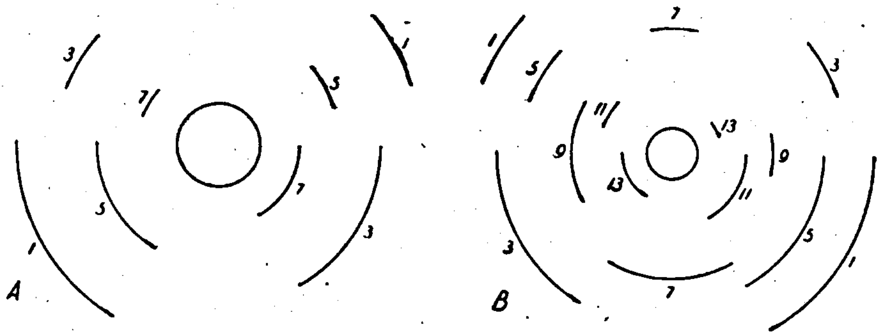

Fig. 34. *Herniaria glabra.* **A = diagram of normal diagonally decussate shoot with small leaves on light side and large leaves on shadow side, B = individual shoot with anomalous succession of leaf pairs.**

the alternating leaf pairs consist of one large under and a small upper leaf, the former being fertile (fig. 34 A). In a particular shoot for instance (fig. 34 B) the large leaves and their axillary branches were present on the right under side in the first, third and sixth node, on the left under side in the second and seventh node, the fourth node bearing a large leaf and a branch on the physiological underside, the fifth on the left side. And a similar case will be described below for *Rhamnus Frangula* in § 33.

Here the relation between the dorsiventrality plane and the leaf pairs had been lost for a moment, to be readjusted immediately, but incidentally in the reverse way. For a better knowledge of the nature of the relation such cases might perhaps be of importance.

2. Changes in the insertion level of leaves or buds.

As dealt with in § 7, in decussate binding whorls the insertion levels of the leaves have to be readjusted.

In many dorsiventral shoots with decussate phyllotaxis no additional changes take place, the leaves of any pair being inserted at the same level, as for instance in *Pellionia pulchra* and in *Columnea gloriosa,* and in order to add a case with median and lateral leaf pairs, in *Crossandra unduliformis.*

In other dorsiventral plants there are however additional shifts of the leaves, consisting of a shift of all leaves of the physiological upper side in a basal or in an apical direction. The former condition is met with for instance in *Colubrina nepalensis,* a Rhamnacea, according to the description by RACIBORSKI (41, p. 22, fig. 10); the latter is to be observed in *Rhamnus Frangula.* In both cases the effect is that alternately two successive leaves are placed on the left and two on the right side of the shoot, which, especially when there is isophylly as in *Rhamnus,* gives a peculiar outward appearance (fig. 35).

Similar shifts are present in the falcate leaves of *Eucalyptus globulus,* the upper leaves being nearly always shifted in the apical direction [1]).

Shifts of the buds, not connected with those of the subtending leaves, are to be observed in an exquisite form in many species of the genus *Cuphea.* The vegetative buds, in this genus subtended by the furthered leaves, remain in their normal place in the leaf axils; the floral buds, subtended by the smaller leaves,

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[1]) The observation is impeded by the fact that in inclined branches there is not always a strict correspondence between the position of the shoot towards light and gravity, as determined from the colours of the stem flanks and from the positions of the leaf blades, and the dorsiventrality phenomena, being the shifts of the leaves, the twists of the petioles and the curvatures of the midribs.

In the Groningen specimen, grown in a tub, this might have been due to variations in the position of the tub, but the same was to be observed in branches from high trees, grown in Madeira.

A special investigation on suitable material of these conditions might certainly be of interest; they may be caused by an early determination of the dorsiventrality phenomena in the bud, while the position of the shoot after its elongation may be changed more or less.

Accordingly in literature the indication of the shift direction of the leaves seems to be failing; al least I could not find it (BRAVAIS 11, p. 21; DELPINO 16, p. 242).

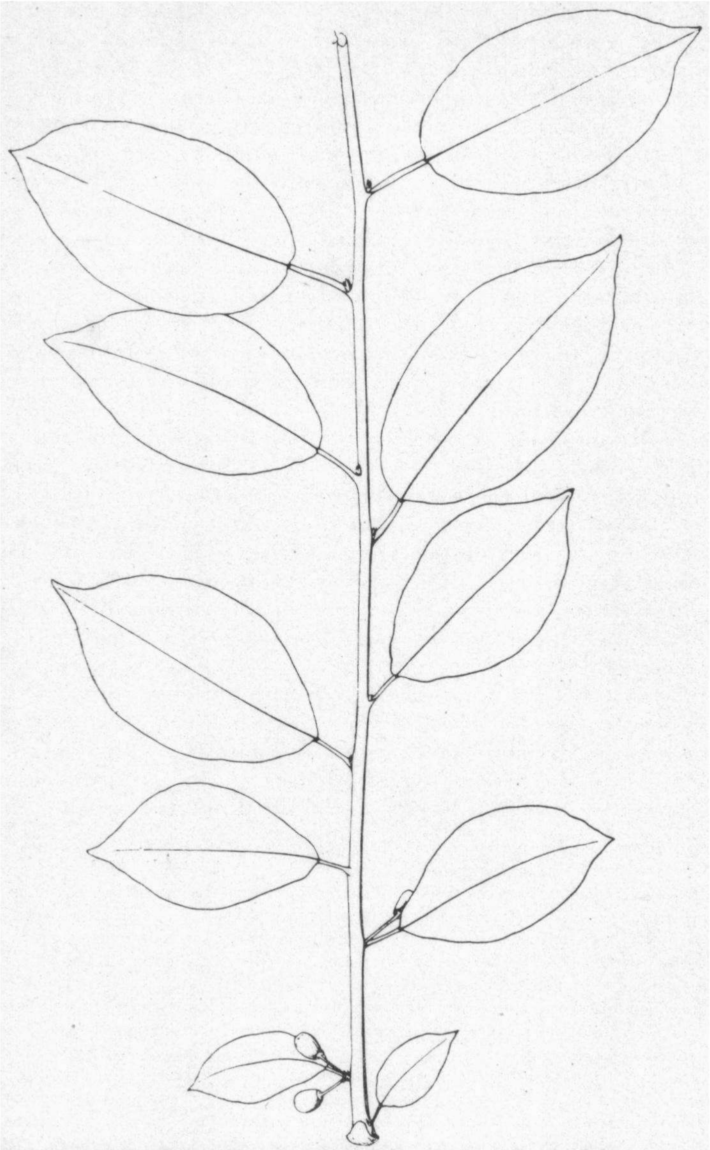

Fig. 35. *Rhamnus Frangula.* Basal region of lateral shoot as seen from light side. Prophylls developed as foliage leaves. Second and higher leaf pairs dissolved by shift in apical direction of upper leaf. $^2/_3$ nat. size.

may be shifted in the apical direction, in many species even up to the next higher node, where they assume a seemingly interpetiolar position; for details and literature see KOEHNE (32).

3. Changes in the angles between the two members of a pair.

In dorsiventral and diagonally decussate shoots it is a very common phenomenon that the opposition of the whorl members is lost by a shift of the two orthostichies of under leaves in the direction of the lateral sides, sometimes even reaching the physiological upper side.

This may be observed for instance in *Goldfussia,* in which the angle between the two orthostichies of under leaves according to BOSHART (3, p. 104) is about 120°, in *Pellionia Daveauana* and *Elatostema sessile* where the under leaves occupy a lateral position and in *Pellionia pulchra* where they are shifted somewhat on to the upper side.

The orthostichies of upper leaves often shift in the same direction, approaching therefore the dorsal median line of the stem; the upper leaves consequently together form a dorsal zigzag line. In *Elatostema sessile* the two orthostichies even approach so much that in the young condition they nearly form one single line, a faint zigzag only still being discernible; in the adult state the same shift still having progressed in the same direction, the zigzag is inverted, the right side upper leaves being inserted on the left and reversely.

4. Changes in the crossing of the leaf pairs.

Of course a change in the angle between the two members of a pair as dealt with sub 3 already affects the crossing of the pairs.

Yet there may be a change in the crossing itself, even in shoots with quite opposed leaves. This is for instance the case in *Columnea gloriosa,* where the diagonal leaf pairs all approach the lateral position, so that the lateral distances between the orthostichies are decidedly smaller than the dorsal and ventral distances.

5. Differences of plastics between the leaves of a pair (anisophylly).

Anisophylly is a very common phenomenon in diagonally dorsiventral shoots.

The difference between upper and under leaves in most cases is restricted to size, the leaves of the upper side being smaller; this difference may be small, as in *Columnea gloriosa,* or more pronounced as in *Centradenia inaequilateralis* where the under leaves have 3—5 times the length of the upper leaves, or finally it may be so pronounced that the upper leaves are hardly perceptible and even may abort. This extreme condition seems to be connected invariably with a shift of the under leaves towards the lateral flanks so that the phyllotaxis in appearance becomes alternating.

In the case of a pronounced anisophylly the difference between upper and under leaves may be more than one of size only, may also pertain to the leaf plastics.

This may be observed for instance in *Pellionia Daveauana* and *P. pulchra,* where the upper leaves are reduced to terete filaments of about 1 mm length and 0.1 mm in diameter. The difference in plastics does not pertain to the axillary stipules, both the large under and the rudimentary upper leaves subtending a single stipule of about 10 mm length.

In *Elatostema* the conditions are similar ¹), with the difference that the reduction of the upper leaves may lead to a total abortion, as occurs in *E. sesquifolia,* the axillary stipules and the axillary inflorescences only indicating the position of the upper leaves; in *E. sessilis* I observed the upper leaves themselves in the shape of a small petiole and a lopsided lamina, together about 1½ mm in length.

A far-going reduction of the upper leaves as described here, is not only to be observed in the *Urticaceae* mentioned above, but has developed independently in a number of other Dicotyledonous families; for a review of these interesting cases I may refer to TROLL (60, p. 398).

The above cases all pertain to anisophylly in diagonally dorsiventral shoots. In the case of median and lateral leaf pairs the dorsiventrality can only pertain to the median leaves. Indeed in *Crossandra unduliformis,* as mentioned above, the median upper leaves are smaller than the under leaves.

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¹) GOEBEL in his Organographie (25, p. 254, 26, p. 341) is opposed to the view of WEDDELL that the visible parts of the upper leaves should be stipules; he writes: "Dies ist nicht richtig; es ist kein Rudiment einer Blattspreite nachzuweisen, und das stipelähnliche Blatt ist ein ganzes, frühe stehen gebliebenes Blatt" and moreover (25, p. 252, 26, p. 340) "Es kommt bei ihnen nicht mehr zur Ausgliederung von Blatt und Nebenblatt (Axillarstipel), und man kann die oberen Blätter leicht mit Nebenblättern verwechseln".

Here GOEBEL is again misled by the deceptive appearance of his developmental observations. If he does not find any division of the leaf primordium into two parts, the lamina and the stipule, this does not mean that such a division does not occur; it must escape all observation in the case where the laminar area, being touched by abortion, does not grow out from the beginning.

6. Differences of plastics between the right and the left half of one and the same leaf (inequilaterality).

In plants with median and lateral leaf pairs inequilaterality of leaves plays an unimportant rôle; only the lateral leaves may be subject to it. In *Thuyopsis dolobrata* according to GOEBEL (25, p. 247, 26, p. 336) the anatomical structure of the light side of the lateral leaves is different from that of the shadow side.

In diagonally dorsiventral shoots asymmetrical leaves are rather common: they may be falcate by a curvature of the midrib, or one half may be broader than the other, the larger half often extending farther downward along the petiole or provided with a basal auricle.

In those cases of which data were available the leaves in diagonally dorsiventral shoots were asymmetrical in the following way: the lateral halves of the under and the median halves of the upper leaves were furthered, or as GOEBEL puts it the + halves are turned towards the upper side of the shoot (25, p. 230, 26, p. 318); for a detailed description see moreover TROLL (60, p. 398).

The under leaves in those cases turn their upper surface to the light without any twist; for the upper leaves a twist is required to bring them into the suitable position. Accordingly, with the exception of the rudimentary upper leaves of *Elatostema sessile* which continue to turn their under side to the light, all assimilating upper leaves turn round by a twist in their petiole. This is for instance very evident in the upper leaves of *Columnea superba* and *C. gloriosa,* where the larger median half turns outward over the smaller half; in *Centradenia inaequilateralis* the twist is only partially executed.

7. Differences between the axillary buds of a leaf pair.

In radial shoots differences in the buds of one and the same whorl may be connected with the differences in age of these buds, as dealt with in § 10. In dorsiventral shoots similar differences may be connected with the position at the shoot sides. Evidently such differences are of some advantage to the plant, and their realization may be reached in different ways.

In many cases the differences are restricted to size; in diagonally dorsiventral shoots the larger leaves usually subtend stronger buds, for instance in *Herniaria. Boerhaavia* in this respect seems to form an exception, as according to the description by WICHURA (67, p. 226) the large buds in the not flowering lower part of the plant are subtended by the smaller leaves.

In many cases however the differences extend to the bud plastics; in *Gmelina parviflora* the lateral leaf pairs of the horizontal branches subtend long secondary branches, the anisophyllous median pairs on the other hand subtend short thorns (RACIBORSKI 41, p. 23, fig. 11).

In shoots with diagonally dorsiventral decussation the two kinds of buds form two zigzag lines, one on the upper, one on the under side. Instances are: *Cuphea* with vegetative buds in the axils of the large, and flowers in the axils of the small leaves (KOEHNE 33, p. 6); *Andrographis paniculata,* with similar zigzag lines, but in the reverse position, the large leaves subtending the flowers, the small leaves the inflorescences (GOEBEL 26a, p. 105); *Hedyotis capitulifera,* with one zigzag of vegetative buds and one of inflorescences (RACIBORSKI 41, p. 41); *Procris laevigata,* with vegetative buds or female inflorescences in the axils of the large and male inflorescences in those of the small leaves (GOEBEL 25, p. 249).

§ 29. Traces of spiral arrangement in dorsiventral binding whorls.

According to the views expressed in the present paper any shoot with dorsiventral binding whorls may be expected to have had originally a spiral phyllotaxis, and it may be asked whether any direct proof for such a view can be given by the demonstration of the presence of actual remnants of such a spiral system.

As such traces are even already lacking in many radial shoots, their presence in dorsiventral shoots, where a new and often powerful disturbing factor is superposed on the binding factors, can be expected only in rare and particularly favourable cases.

Yet, when irrefutable, even feeble traces are sufficient to give evidence of the correctness of the theory advanced, and in chapter 6 we shall see that at least a few cases really have been observed.

A description of the observed facts and a discussion of their bearing on the theoretical interpretation will be given in the next chapter.

CHAPTER 6. DORSIVENTRAL BINDING WHORLS IN SOME SPECIAL PLANT GROUPS.

The present chapter, intended to parallel our third chapter on radial binding whorls in some plant groups, will have to remain very fragmentary, on account of the scarcity of suitable material.

Indeed, though the number of plant species with decussate and dorsiventral shoots is large enough, and several of these species are readily available, most of them do not answer our purposes.

Plants with unlimited vegetative shoots in which moreover hardly any deviations from the normal decussate phyllotaxis occur, do not offer any opportunity for recognizing a possible original form of phyllotaxis.

What we need for our investigations are such species in which the shoots have dorsiventral binding whorls, and at the same time still show traces of the original phyllotactical pattern.

Theoretically this might be realized in different ways.

In the first place both the dorsiventrality and the binding might be so weakly expressed that the original phyllotaxis was still more or less evident.

In the second place we may have regionally different plastics in one and the same shoot, dorsiventral binding for instance occurring in the lower region, the upper part having neither dorsiventrality nor binding. In such cases the transition to the second region, especially if brought about gradually, might answer the purpose.

In the third place we may have a plant forming two kinds of shoots, one being radial and spiral, the other having dorsiventral binding. As in nearly all plants transitional forms between such shoots are formed sometimes, these might be useful to us.

Of the first possibility no instances have come to my knowledge.

The second is to be expected especially in plants with terminal inflorescences or terminal flowers, if the latter are radial. As however most dorsiventral plants have unlimited shoots and axillary inflorescences or flowers (*Cuphea, Linnaea, Eucalyptus, Centradenia, Pilea, Elatostema*), the choice of suitable plants is much restricted.

WYDLER gave some promising descriptions of *Epilobium montanum* (74, p. 222), *Circaea lutetiana* (ibid. p. 223) and *Saxifraga oppositifolia* (id. p. 388, 754).

In these three species the described facts amount to the same: a decussation which is dissolved in the upper part of the shoot and merges into a spiral arrangement in the inflorescence (*Epilobium* and *Circaea*) or in the calyx of the terminal flower (*Saxifraga*). The solution in the upper part of the shoot takes place in such a way that the lower leaves of the pairs form a ¼ spiral; still higher the bracts in the inflorescence of *Epilobium* and *Circaea* and the sepals in the terminal flower of *Saxifraga* display a normal spiral arrangement which fits in with the dissolved pairs.

Notwithstanding these facts which would have been normal in a plant with radial shoots, the buds subtended by the foliage leaves are placed in a zigzag as in dorsiventral shoots.

It is clear that such a relation means that the shoot is slightly dorsiventral but at the same time by the solution of the leaf pairs exhibits the origin of the whorls from a spiral pattern. It was therefore particularly important to check the correctness of Wydler's statement.

In *Circaea* I did not succeed, as the plants as growing in Groningen have hardly any leaf pair solution and especially as the bractless flowers are distributed quite irregularly, so that the course of the spiral of the aborted bracts cannot to be determined. *Saxifraga oppositifolia* was not at my disposal, but in *Epilobium montanum* I was happily able to confirm Wydler's description to the full, as will be described below.

Moreover *Helianthemum apenninum* will be dealt with, and also the nearly related genera *Herniaria* and *Paronychia,* all having radial flowers with an imbricate pentamerous calyx, and dorsiventral and decussate foliage leaves below the terminal flower.

Fraxinus should belong to the third group of cases according to the descriptions of Dutrochet and of Wydler; as we found however above in § 21 that *Fraxinus,* the classical instance of dorsiventral decussation, is not dorsiventral at all, we can no longer make use of it here.

About *Acer campestre* Dutrochet reports exactly the same facts as about *Fraxinus* (18, p. 213) and Wydler adds that in shoots with a zigzag distribution of lower and higher leaves in the pairs, the lower leaves may be larger, so that the shoot becomes anisophyllous (82, p. 54). So the case is promising, but as I did not succeed in observing shoots with dissolved leaf pairs, I could not examine it.

A third case, that of *Rhamnus Frangula,* will be dealt with below.

§ 30. Epilobium montanum.

Of this species Wydler wrote: "die Laubblätter des aufgeschossenen Stengels stehen Anfangs paarweise, lösen sich aber höher theils mit Beibehaltung ihrer rechtwinkligen Stellung, theils in $^3/_5$ oder $^5/_8$ St. übergehend auf. So weit die aufgelösten Blätter noch rechtwinklig stehen, entspricht ihre Ordnungsfolge derjenigen oben bei *Epilobium parviflor.* angegebenen (i.e. first leaves in ¼ spiral); jedoch kommen öfters Metatopien vor. Nicht selten findet man an Exemplaren, wo die Blätter paarig opponirt stehen, ungleich grosse Achselsprossen, aber seltsamerweise ist dann die Sprossstellung nicht wie z.B. den Caryophylleen, sondern wie bei *Herniaria, Linnaea, Cuphea,* manchen Labiaten, Acanthaceen etc., nämlich so: (wo die Buchstaben die Blattpaare, + und — die ungleich grossen Sprossen bedeuten)

	B+			3,	
	D+			7,	
	F+			.	
	.			.	
A+ C+ E+ .		. E– C– A–	1,5,9 . .		. . 10,6,2,
	.			.	
	F–			.	
	D–			8	
	B–			4	

Die aufgelösten Blattpaare gaben hierbei kein sicheres Resultat, denn der +Spross gehörte bald dem untern, bald dem obern Blatte an, doch schien der +Spross etwas häufiger in der untern Blattachsel zu stehen. Nehmen wir an, der +Spross gehöre dem ersten Blatt des Paares an, so würde sich obiges Zahlenschema gestalten" (74, p. 222).

Thus we see that for Wydler the zigzag position of the buds is a more basic phenomenon than the ¼ spiral of the lower leaves; this will be discussed presently.

From a description of *Epilobium montanum* by Zimmermann (86, p. 277) we may gather that in his material the shoot and the solution of the foliage leaf pairs had the dorsiventral form, the leaves of two adjoining orthostichies being larger and inserted at a higher level; at the same time the author found convergences in the pairs, ascending in a ¼ spiral (p. 279).

Though differing in detail, the two descriptions by Wydler and by Zimmermann agree therefore in the indication of a combination of dorsiventrality phenomena with a spiral; the same was observed, though again in a different form, in my own material.

In my plants the shoots without a single exception were strictly decussate in the region of the large foliage leaves; in the higher regions the smaller leaf pairs on the other hand were dissolved in a regular way without any metatopies, the lower leaves of the pair forming a ¼ spiral. Finally by the loss of the rectangular crossing the arrangement merged into a normal spiral phyllotaxis of the bracts.

No indications of any dorsiventrality were to be observed in the stem or in the leaves, and in strong shoots all branches were equally developed on all sides, without any distribution of the branches in a zigzag or in a spiral. In poor shoots no branches being developed at all, it was in the medium-sized shoots that the two branches of a pair were often strikingly different in size, and then these differences often were distributed in the way described by WYDLER, though exceptional nodes did not fail to occur in which it was the opposed branch which was the stronger.

Out of 9 shoots in which three or more nodes showed such branch differences, no less than five had a clear zigzag of their branches and four showed one or two exceptions.

When I numbered the branches according to the order of their subtending leaves in the original spiral, as below

3
8
11
16
19
1 6 9 14 17 . 18 13 10 5 2
20
15
12
7
4

I got the following results.

In the five specimens with a branch zigzag the buds were: 2, 3, 5, 8; 1, 4, 6, 7, 9; 2, 4, 5, 7, 10; 1, 3, 6, 8, 9; 2, 4, 5, 7, 10, 12. It is therefore clear that there is no relation between the original spiral and the orientation of the bud zigzag.

In the four exceptional cases the buds were: 1, 6, 10, 11, 16, 20; 1, 4, 5, 8, 10, 12; 1, 3, 7, 10; 1, 3, 5, 8, 10, so that the buds were placed on four or three sides of the stem. These cases did not represent any approach to a radial distribution in a ¼ spiral; for such a distribution the branches in one specimen should either all have had odd or all even numbers.

So we see that while the leaves are radially decussate, the shoot must have a small amount of dorsiventrality to the effect that the buds on one side of the shoot have a more pronounced tendency to develop.

WYDLER's supposition that the real genetic order of the leaves is indicated by the position of the strong buds, is consequently not supported by our observation of the irregularities in the bud distribution; on the other hand the spiral order of the bracts is always quite regular, and the leaf pair solution corresponds always or nearly always to it.

Therefore our conclusion must be that the shoot of *Epilobium montanum* represents a slight degree of dorsiventrality, but that at the same time the original spiral of the decussate leaves has left clear traces, a fact which is especially important for our theoretical views.

§ 31. Helianthemum apenninum.

In the genus *Helianthemum* a small amount of diagonal dorsiventrality may be present in the leafy shoots.

The stage of anisophylly never seems to be reached, but the development of a zigzag of buds on the light side of the inclined shoot, is a striking feature of many species.

WYDLER, though mentioning "viele *Helianthema*" (68, col. 213) as having a ¼ bud spiral, later records "einzelne Arten von Helianthemum" (76, p. 206), and still later (84, col. 822) even simply "Helianthemi sp." as having the Labiate type, i.e. the dorsiventral decussation.

The latter type is certainly present in *Helianthemum apenninum*; the bud zigzag, though subject to many deviations, yet on the whole is very conspicuous.

When the terminal inflorescence is formed, the decussation usually gives place to a very short spiral part; this may comprise only one or two leaves (compare WYDLER 83, p. 315).

In the case of a spiral part of two leaves these two are inserted at different levels, they are not opposed but diverge about 137° and moreover their plastics are different, the lower one being a sterile foliage leaf with two stipules, the higher one being a bract without stipules, subtending the second flower of the cincinnus.

When the spiral part is restricted to one single leaf, this has the plastics of a bract, it subtends the second flower, and it is either situated right between the last two foliage leaves or nearer to one of them, indicating in this way a spiral sequence of three leaves.

On comparing the direction of the spiral thus found with the contortion directions of the calyx and the corolla of the terminal flower, we find almost invariably the correspondence which might be expected, namely that a right winding spiral is followed by a left contort calyx and a right contort corolla (49, p. 43). In my observations this was found in 23 out of 25 cases. So we see that as soon as the dorsiventral decussation disappears a spiral phyllotaxis makes its appearance which is continued in the floral phyllomes.

For the proof of the spiral origin of the dorsiventral decussation to be convincing we ought to find the course and the direction by other means, so as to compare it with the spiral as determined in the way described above.

With this aim I traced the spiral direction in a number of branches developed from buds placed on the right in the zigzag and from another number placed on the left; if we could have found that all branches of the right side had the same direction in their phyllotactical spiral and those from the left side the reverse direction, it would have been established that, as often occurs in dorsiventral shoots, the leaf spiral of the new buds should have been determined with respect to the dorsiventrality plane of the parent axis.

The observation however showed clearly that such a relation did not exist; branches from opposed leaves of the same pair sometimes were even homodromous. Evidently the dorsiventrality of the parent axis being weakly expressed, the buds were poecilodromous.

§ 32. **Paronychia and Herniaria.**

For the purpose of studying the phyllotaxis of these genera cultures were grown in the Groningen Hortus during the years 1932 and 1933, comprising *Paronychia arabica, argentea, bonariensis, echinata, polygonifolia, Herniaria caucasica, cinerea, glabra, hirsuta, incana* and *latifola.*

As the differences between the species in morphological respect were of small importance, a general treatment will be given here.

The primary axis of the seedling begins in all cases with two isophyllous and decussate leaf pairs, namely with the glabrous cotyledons and the often more or less pilose plumular leaves. The epicotyl being always short, the four leaves are inserted at about the same level. Above the first plumular pair, or the second leaf pair as it will be called here, the internodes are well developed, forming a more or less procumbent stem with decussate leaf pairs which are either provisionally isophyllous (*Paronychia*) or directly anisophyllous (*Herniaria*). After a varying number of leaf pairs, the shoot is terminated by a terminal flower.

The ramification of the plant is mainly provided for by the strong development of the buds from the second leaf pair; in *Paronychia* those from the cotyledons grow out too and are nearly as strong. By the development of some basal laterals of these branches, a varying number of strong supplementary branches is formed, and by the loss of the lower leaves the morphological analysis of the complex of strong branches, all procumbent and radiating from the hypocotyl, soon becomes very difficult or impossible; as a rule it is even impossible to distinguish the main axis from its laterals.

The strong branches formed in such a way in their turn form numerous laterals, the morphological relations of which may be easily stated. And as their distribution is determined in a very strict way, this will be dealt with first.

All vegetative leaves being opposite, the leaf pairs are placed diagonally on the dorsiventral shoot. In *Paronychia* there is a small amount of anisophylly, in *Herniaria* the same is strongly expressed; in both the upper leaves are the small, the under leaves the large leaves. The pairs do not cross rectangularly, as all four orthostichies are rather strongly shifted to the right and left side.

In the vegetative part the well known membranaceous stipules are always fused, so as to form two interpetiolar stipules for a pair, in the same way as in most *Rubiaceae*. In the leaf pair under a terminal flower they may be free, so that three or four of them are present at a single node. And in the dichasial part they are all free and they are even present in such cases where the leaf itself aborts.

The under leaves usually being the only fertile leaves, the branches are placed alternately on the left and on the right side. In the last leaf pair under a terminal flower the large under leaf subtends an extraordinarily strong branch which is sympodial, and here the upper leaf is fertile too, subtending a branch of about the same size as that of the next lower under leaf.

By these facts the regular alternation of the laterals of every strong branch is seemingly once disturbed, namely at the node where the first terminal flower is to be found, as our Pl. 1 may illustrate.

The photographed object is the apical part of one of the strong branches of *Herniaria incana,* seen from the light side.

At the first node, at the top of the photo, we see two withered leaves, a small one on the left, a larger one on the right, the latter subtending a lateral branch. At the second node the small leaf is fresh, the large being withered; the branch is from the latter. At the third node the branch seems to be again on the left; in reality the fresh large leaf on the right subtends the sympodial branch, the small and withered leaf the weaker branch, the terminal flower being visible in between.

As the strong sympodial branch at its first node again forms a sympodial branch from its large, and a smaller branch from its small leaf, a new alternation of branches on the right and the left is initiated. It is exactly by this apparent interruption of the regular alternation which always recurs in the same way, that it is easy to find immediately the terminal flower of any vegetative axis.

These facts having been stated we may ask in how far *Paronychia* and *Herniaria* may be serviceable for the study of dorsiventral decussation. As their flowers are radial, usually pentamerous and have a quincuncial calyx aestivation, we may derive the direction and the course of the original spiral from them. And as the spiral, determined in such a way, may be traced back into the decussate part we may try to compare it there with other morphological phenomena.

It soon appeared that at least the main axis of the plant could not be used, owing to the technical difficulty that the terminal flower of the main axis only opens at a time when all lower leaves have disappeared already and the morphological analysis of the basal branch complex is no longer possible.

So I had to confine my observations to the laterals and in these we have to distinguish between "plurinodal" and "uninodal" branches, as *Wichura* called them (67, p. 232, "mehrgliedrig" and „eingliedrig"), the former having more than one pair of vegetative leaves, the latter only one pair of leafy prophylls. The latter occur in great number in the dichasial part, the former in the basal vegetative part of the strong branches.

In Pl. 1 is is clear that only uninodal branches are present, the two laterals of the vegetative region even bearing flowers at their first nodes.

In the uninodal branches it often occurs that one of the prophylls, or both, abort wholly. Yet in such cases their positions may be clearly recognized from their axillary products, and from their persisting stipules.

Owing to the diagonal form of decussation of the parent axis, the lateral prophylls of the branches are directly placed in the position of an upper and an under leaf. From the calyx aestivation it is easy to state that in uninodal branches the upper leaf is the α-, the under leaf is the β-prophyll; see fig 36.

For their development we have the following rules. When developed, they have the plastics of upper or under leaf, according to their position. Moreover we have in *Herniaria* the additional rule that all α-prophylls always abort. And in both genera we have that in the condensed inflorescence parts, the glomerules, all prophylls abort; and the same may be the case in the basal nodes of a lateral sympodial axis, though not condensed.

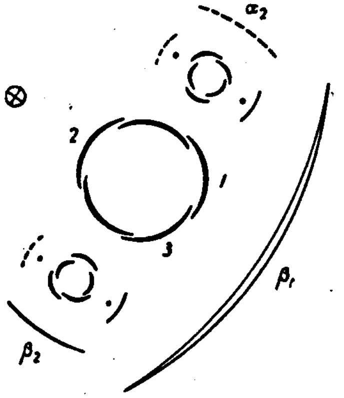

Fig. 36. Diagram of dichasium branch of *Herniaria;* of the dotted α-prophylls only the stipules develop.

This may be illustrated by a consideration of some parts of our Pl. 1. The first lateral on the right consists of a developed internode and a node bearing no prophylls but only a peudo-terminal abaxial β-branch and an α-branch and moreover a terminal flower which is hidden in a basal glomerule of the α-branch. This α-branch has a very short basal internode where by way of exception the fertile β-prophyll is developed, subtending the second sympodial member of the α-branch, of which the internode is visible and the new β-prophyll and a new glomerule.

We see at the same time that the position of the β's is alternately on the right and on the left in the successive sympodial members of the α-branch, and the same will be met with everywhere, in consequence of the fact that all β-branches are antidromous to their parent axis.

On determining the calyx aestivation in a number of such uninodal branches, it soon becomes clear that all α-flowers are homodromous, all β-flowers antidromous to their parent axis, as might have been gathered already from the prophyll positions, and moreover that the genetic spiral always runs opisthodromously from α to β. In other words, the dichasium is constructed on the same lines as in all other *Caryophyllaceae.*

This proves that the calyx aestivation is eutopic, and that it may be used as a solid basis for the determination of the spiral in plurinodal branches. So the latter were investigated on a somewhat larger scale.

As all plurinodal branches arise as laterals from the under side of clearly dorsiventral shoots, we might expect beforehand that they would have an original phyllotactical spiral of a determined and fixed course, all left laterals having the same spiral and all right laterals having its mirror-image: we find for instance in Wichura the sentence: "dass zwischen den Knospen, welche in einer continuirlichen und denen, die in einer gebrochenen Spirale übereinander gereiht sind, ein bemerkenswerther Unterschied stattfindet. Die ersteren bringen Zweige hervor, welche bald mit dem Centralstengel entweder sämmtlich homodromisch oder antidromisch, bald theils homodromisch, theils antidromisch sind, ohne dass es letzterenfalls möglich wäre, ein bestimmtes Gesetz für die Aufeinanderfolge der ungleichläufigen Knospen ausfindig zu machen. Von den zu einer gebrochenen Spirale gehörigen Knospen ist dagegen eine jede mit der nächst vorhergehenden und nächstfolgenden symmetrisch oder antidromisch, so zwar, dass die symmetrischen in je zwei Reihen einander gegenüber, die congruenten aber über einander zu stehen kommen." (66, p. 166).

My observations however soon taught me that the laterals from both sides promiscuously had right and left-handed spirals without any perceptible rule. So the conclusion seemed obvious that the laterals should be poecilodromous, their spirals being determined by change only.

As this result seemed strange in a plant with clearly dorsiventral shoots, the observations were continued and the records were put together in different ways. Suddenly the chaos cleared up, as soon as the binodal, trinodal, quadrinodal etc. branches were classed as separate groups; with the exception of a very few cases which evidently were due to errors in the difficult and ticklish observation, all cases of the same class had exactly the same form of spiral, as follows.

Fig. 37, 1 gives the uninodal branch, as described above; the

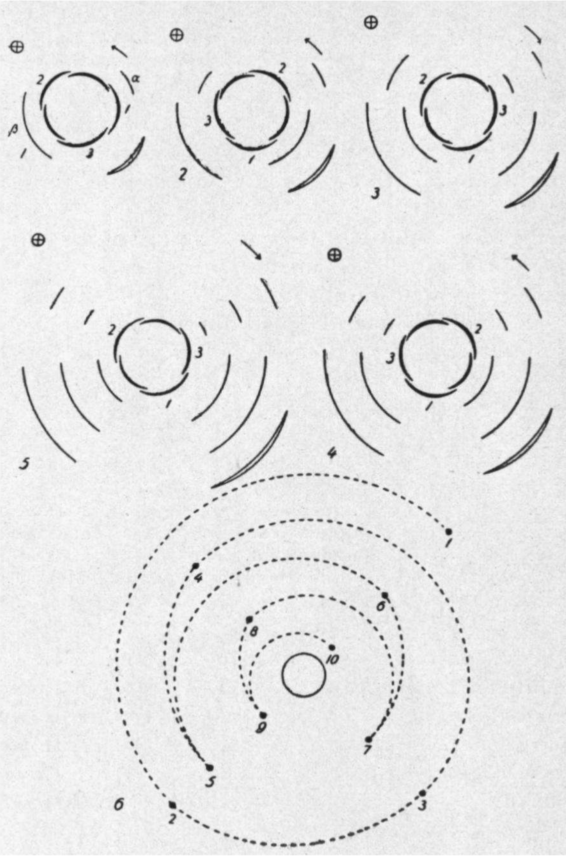

Fig. 37. Diagrams of lateral branches of *Paronychia* and *Herniaria.* 1 uninodal branch; 2—5 binodal-quinquenodal branches, 6 course of phyllotactical spiral as derived from the different modes of calyx aestivation.

direction of the calyx spiral has been indicated by an arrow. Fig. 37, 2 gives the binodal branch; we see that the spiral runs as in the uninodal branch, and that by the intercalation of another leaf pair the position of the terminal flower has rotated through 270°.

Fig. 37, 3, the trinodal branch, on the same principles should have had a dextrorse spiral like 1 and 2, with sep. 2 on the abaxial side. Instead it has a sinistrorse spiral with sep. 2 on the adaxial side.

Fig. 37, 4, the quadrinodal branch, has again a dextrorse spiral with sep. 2 in the same position as in the binodal branch, whereas in Fig. 37, 5, the quinquenodal branch, the calyx is again sinistrorse with the same position as in the trinodal branch. In branches with more nodes the calyx positions alternate in the same way; branches with 7 nodes having the same position as those with 3 and 5, those with 6 and 8 the same as those with 4.

When tracing back these different calyx spirals through the preceding leaves, we get the curious result that this supposed spiral starts from the prophylls in all four possible ways: from an upper or an under leaf and opisthodromously and emprosthodromously, in the way as indicated below.

Number of nodes under terminal flower	Supposed spiral in vegetative region	
	starts from	runs in first node on the
1, 2, 6 etc.	upper leaf	adaxial side
3, 7 etc.	upper leaf	abaxial side
4, 8 etc.	under leaf	abaxial side
5, 9 etc.	under leaf	adaxial side

These curious results were observed in:

Paronychia arabica	in 10	out of 13 flowers
P. argentea	5	6 flowers
Herniaria glabra	12	12 flowers
H. glabra verticillata	7	7 flowers
H. hirsuta	30	31 flowers
H. incana	2	2 flowers
Together	in 66	out of 71 flowers.

So the result in itself must be considered as well established; and we must now try to understand it.

In the first place we may remark that, as fig. 37 shows, in the plurinodal branches the calyx aestivation has only two forms, and that in all cases sep. 3 and 5 are turned towards the upper, sep. 4 towards the under leaf of the last vegetative whorl, so that we get the impression that it is the last vegetative whorl which determines the calyx aestivation, irrespective of the number of preceding nodes.

In the uninodal branches on the other hand the conditions are different, sep. 1 and 4 being turned towards α and 5 towards β. And as we saw that in these uninodal branches the aestivation undoubtly is eutopic, there is no reason to suppose that it should be metatopic in the plurinodal branches. The only way to reconcile these facts is the supposition that in the plurinodal branches the spiral is reversed at every third leaf, to begin with leaf 5, as has been drawn in fig. 37, 6.

Such a reversal of the spiral which was assumed by BRAUN, by WICHURA and by WYDLER to be of normal occurrence in all dorsiventral shoots with decussate leaves, at first sight not only seems decisive against the present author's view of the origin of dorsiventral decussation by metatopic changes, brought about in a common spiral phyllotaxis, but it seems even to refute the view of a previous determination of the leaf centres by dispersion circles, to be followed by independent growth phenomena, initiating the leaf primordia. For it might seem that the mode of development of these leaves, whether alike on all stem sides or different on opposed sides, can never influence the original predetermined system of leaf centres.

Yet, after some consideration it appeared to be possible to give a rather simple hypothetical explanation which might wholly cover the observed phenomena, an explanation based on nothing but physiological principles.

If we assume that the ventral and the dorsal sides of the stem are different in their morphogenetic forces, even above the level of the youngest leaf centres, the induction of new leaf centres and the formation of new dispersion circles have to take place in different circumstances on the dorsal and the ventral sides, and if we then suppose further that on the dorsal side, where later the reduced leaves will arise, the dispersin of "leaf agency" (cf. 46, p. 320) is impeded or reduced in some way or other, phenomena of the kind described above may be the result, as will be shown by the following instance.

For simplicity's sake we do not suppose that the reduction of the dispersion circles on the dorsal side is due to an increased resistance of the meristem to leaf agency, as in that case the dispersion surfaces would cease to be circles and have to assume complicated forms; we assume that the production of leaf agency is smaller at the dorsal side, but that all dispersion surfaces remain circular.

Our fig. 38 A represents the unrolled surface of a dorsiventral shoot; the hatched longitudinal zone represents the dorsal stem side, and the dispersion circles are supposed to have a radius of 0.45 on the ventral, 0.25 on the dorsal side, both expressed in terms of the stem circumference.

When once realized, the construction may be continued by simply adding new circles of the indicated sizes, and it will continue to give an oscillating sequence of leaf centres, reversing at every third centre.

The beginning of the system has been realized here by drawing a single circle round the first centre with a radius of 0.31, and another round the second centre with the radius 0.45, in the appropriate positions. It might have done however in

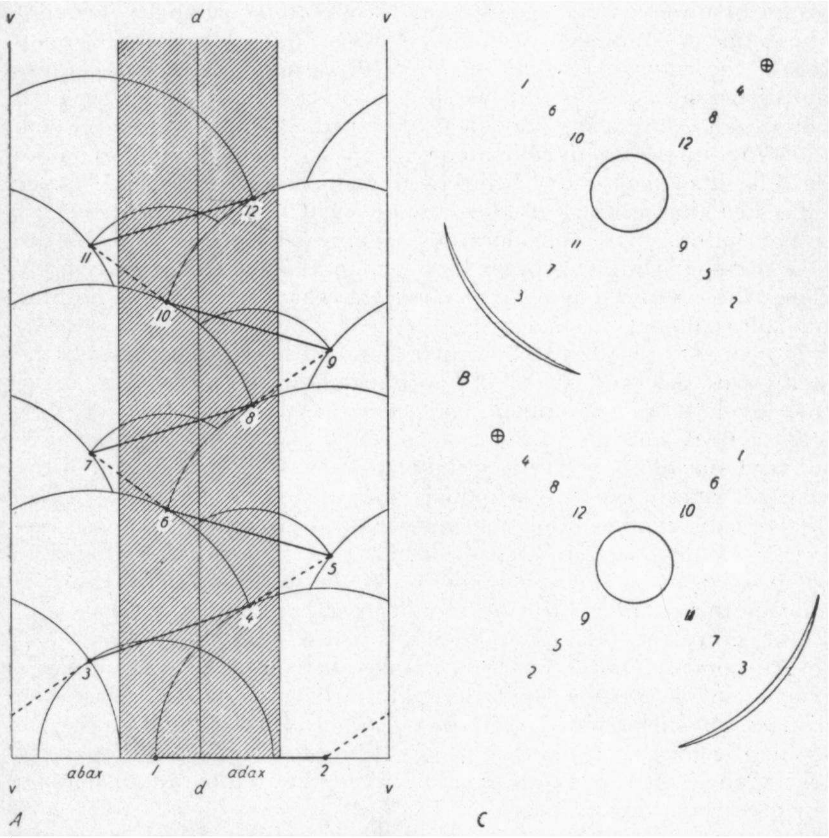

Fig. 38. *A,* junction scheme of dispersion circles for lateral branches of *Paronychia* and *Herniaria,* based on the supposition that the circles on the dorsal side *d* (hatched) are smaller than those on the ventral side *v* (white). Leaf pairs indicated by continuous lines, genetic order of leaves by continuous lines + dotted lines. *B* and *C* diagram of same phyllotaxis in its two antidromous forms.

different ways, but as fig. 38 is purely hypothetical and nothing but an instance, it is useless to strive after a too close correspondence to the actual conditions.

In the system, represented in fig. 38 A, dimerous binding whorls may be formed, and if then further the leaves on the dorsal side remain smaller than on the ventral side, a phyllotaxis like that of *Herniaria* and *Paronychia* is realized, as represented in its two antidromous forms in fig. 38 B and C.

When we further suppose that at a certain level both the binding and the dorsiventrality disappear, as must be the case when the shoot forms its terminal flower, our construction of fig. 38 has to be continued by means of circles all of the same size.

Consulting our fig. 38 A, we recognize that when the circle around 10 is the last small circle and that around 12 is of the full size, a system 1 + 2 with right winding spiral ensues. But if the circle round 10 had been full sized already, a similar system with a left-hand spiral would have been the outcome.

The difference, described in the actual specimens between the uninodal and the multinodal branches, is also paralleled in fig. 38 A, by the fact that no reversal takes place at leaf 3. Thus we may get a close parallel between the construction and the actual conditions, if we assume that the dorsiventrality and therefore the difference in size of the dispersion circles disappears in the last foliage leaf pair.

A full sized circle around centre 10 means as we saw, a left-hand spiral above it. This corresponds to fig. 37, 5, leaves 1 — 10 forming five leaf pairs, and the calyx being formed out of 11 — 15, with a left-hand spiral.

In the same way fig. 37, 4 corresponds to a full sized circle round centre 8, and a calyx from 9 — 13; 37, 3 corresponds to a full sized circle round 6, and 37, 2 to one round 4. But the circle round 2 is already full sized and even a large circle round 1 does not change the spiral direction when 1 keeps its same place at the left margin of the circle round 2.

Of course I do not pretend to have given a full explanation of the curious facts observed in these plants. Fig. 38 only intends giving a rough model of the unknown conditions; but it proves that it is not necessary to have recourse to the assumption of any metaphysical forces.

§ 33. Rhamnus Frangula.

About the phyllotaxis of *Rhamnus Frangula* WYDLER wrote:

“Blätter oft nach 3/5 zuweilen paarig decussirt .... die Paare aufgelöst, aber mit manchen Anomalien” (73, p. 456). But six weeks later he wrote (ibid. p. 559): “Nach kürzlich nochmals vorgenommener Untersuchung der Blattstellung stellt sich heraus, dass dieselbe (auch noch leicht an Axen früherer Jahrgänge sichtbar), — allgemein die paarig-decussirte ist, wobei die Paare durchweg aufgelöst, recht-, selten spitzwinklig sind, und zwar die Auflösung dem oben bei *Evonym. europ.* gegebenen Schema (i.e. in a zigzag) entspricht. So zählte ich oft an längern continuirlichen, mehreren Jahrgängen angehörigen Axen bis 25 aufgelöste Blattpaare in schönster Ordnung. Jedoch fehlte es nicht an Anomalien, wo einzelne Paare umgewendet erscheinen, was vielleicht durch ungleich hohes Anwachsen der Blätter bewirkt wird. Gegenüber stehende Zweige zeigen nicht selten gegenwendige Blattstellung. Merkwürdig ist dabei das Verhalten des ersten Blattpaares (der Vorblätter), wie folgendes Schema zweier einander gegenüberstehender Zweige zeigt:

$$\mathrm{B}\left\{\begin{array}{ccccccccccccccccc}
&&&& A^2 &&&&&&&&& A^2 &&& \\
&&&& C^1 &&&&&&&&& C^1 &&& \\
&&&& E^1 &&&&&&&&& E^1 &&& \\
&&&& G^1 &&&&&&&&& G^1 &&& \\
B^1 & D^1 & F^1 & H & . & H^2 & F^2 & E^2 & B^2 & \mathrm{A} & B^2 & D^2 & F^2 & . & F^1 & D^1 & B^1 \\
&&&& G^2 &&&&&&&&& G^2 &&& \\
&&&& E^2 &&&&&&&&& E^2 &&& \\
&&&& C^2 &&&&&&&&& C^2 &&& \\
&&&& A^1 &&&&&&&&& A^1 &&&
\end{array}\right\}\mathrm{B}$$

A. Abstammungsaxe der beiden aus den Blättern B entspringenden gegenüberliegenden Zweige. A1 A2 B1 u.s.w. gibt die Anordnung der Blätter dieser Zweige an. Anstatt dass hier das Blatt C1 über A1 fällt, steht vielmehr über diesem Blatt C2 und alle folgenden zweiten Blätter derselben Zeile”.

For my own investigation I had at my disposal a practically unlimited number of shrubs in the wild state; all WYDLER’s results, both the earlier and the later, though they seem more or less contradictory, were fully confirmed.

We have for instance the rule that all erect stout shoots and especially those arising as gourmandizers after the cutting of the main stem, invariably have a regular spiral phyllotaxis, without any trace of whorl formation or of dorsiventrality. Usually they are even devoid of metatopic disturbances.

On the other hand the great majority of shoots in any shrub is decussate and at the same time diagonally dorsiventral, and then we have very few exceptions to the rule that the leaves of the two rows on the light side are shifted in the apical direction, so that at first sight the appearance is that the shoot has alternately two successive leaves on the right and then two on its left (fig. 35).

The shifts of these leaves are sometimes so great that the distances between the leaves of the pairs become equal to those between the pairs, and consequently the pairs are only to be recognized by the opposition of their members; usually however the shifts are less, so that the pairs still may be recognized at first sight (fig. 35).

The upper and under leaves have the same plastics, but their size is not exactly the same, though the difference is very small and not always well expressed; on the whole however the under leaves are somewhat larger in size than the upper leaves.

The inspection of the apex of such a shoot in the growing state reveals the fact that the upper leaves are not only shifted in the apical direction, but that when compared with their partner they are decidedly behind in attaining their full size. So if these dorsiventral shoots originally have a spiral phyllotaxis, the longitudinal shifts must be such as to bring with them an earlier development of the leaves shifted towards the base and a later development of those shifted towards the apex.

At the base of the shoots we sée that according to WYDLER's description the first leaf pair has a level difference in the reverse sense, so that the shoot begins with three seemingly alternating leaves (fig. 35). As however the lower leaf of the first pair usually is only present in the shape of a small scale, and the second leaf sometimes too, this feature is usually not so prominent as in the figured specimen, where all phyllomes have been developed as foliage leaves.

In lateral branches, borne themselves on dorsiventral branches, the position of the leaf pairs is subject to a rather strict rule, expressed in our diagram fig. 39; the adaxial side of the lateral branch, indicated by an arrow, in the expanded condition is turned towards the light, and in any branch the first phyllome is situated on the light side of the parent axis.

On comparing this fig. 39 with fig. 38, a striking correspondence of the conditions is found. Indeed the conspicuous arrangement of the leaves on the lateral shoots of *Rhamnus Frangula* is almost identical with that, derived on a theoretical basis for the shoots of *Paronychia* and *Herniaria,* the only difference being the crossing at an acute angle of the first and the second leaf pair in *Rhamnus.*

So the question rises whether the phyllotaxis in *Rhamnus*

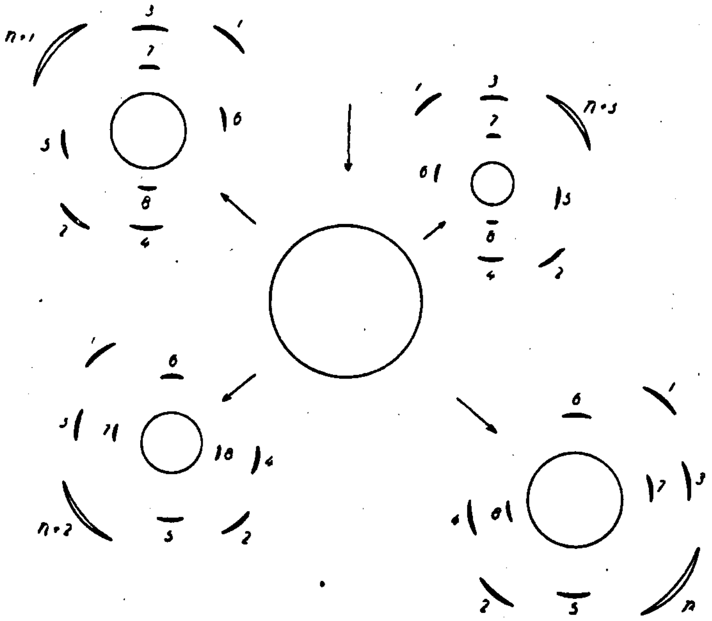

Fig. 39. *Rhamnus Frangula.* Diagram of diagonally decussate branch system. Arrows indicate the adaxial sides of the branches which turn to the light. The leaves in the pairs being inserted at different levels, the numbers indicate their insertion order.

Frangula has to be explained like that in *Paronychia,* and has to be taken as an originally zigzag arrangement.

This question is the more puzzling as one might expect that the phyllotaxis of *Rhamnus Frangula* should be nothing but a dorsiventral decussation, due to the origin of dimerous binding whorls in a system of the main series, the zigzag having been conditioned by a shift of the light side leaves in the apical direction (or the shadow side leaves in the basal direction).

As the latter explanation is much more simple, and the existence of shifts in dorsiventral shoots is put beyond doubt by cases like that of the flowers in *Cuphea* spp., it seems at first sight more attractive.

On the other hand we have the remarkable fact of the reverse slope of the first leaf pair, occurring in *Rhamnus* in exactly the same form as postulated for *Paronychia;* a fact pointing in the direction of the former alternative.

When we turn now to the occasionally occurring anomalies, we shall see that we are not helped to make a deliberate choice between the two possibilities.

In the first place we may examine the rather numerous cases, already mentioned by Wydler, in which the leaf pair solution is irregular, isolated leaf pairs having a reverse solution. As these cases were distributed without any noticeable rule as far as I was able to make out, they did not give any information. Only one other anomaly deserves to be considered here.

This was a lateral shoot below a dead main apex. The arrangement of the three first leaf pairs being normal (fig. 40) the fourth (7, 8) and the fifth pair (9, 10) occupied anomalous positions, the fourth in the median plane, the fifth above the second pair.

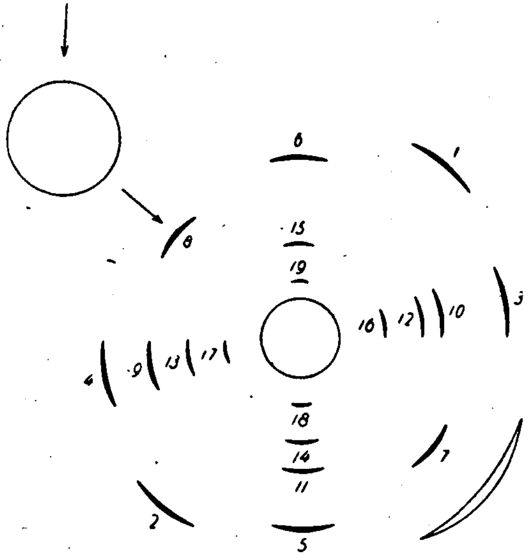

Fig. 40. *Rhamnus Frangula.* Diagram of particular shoot with abnormal orientation of leaf pairs. Leaves numbered according to insertion levels.

Above the fifth pair came an odd leaf 11 on the under side; the subsequent pairs alternated normally. So the relation between dorsiventrality and decussation was restored in a modified way.

In my opinion the case proves that the whole arrangement cannot be simply the outcome of junction phenomena; it must be due to a brief disturbance of unknown nature, interrupting the binding and changing the relation between leaf orthostichies and dorsiventrality plane. A discrimination between the two possibilities quoted above cannot be derived from it.

In the second place we may observe rare cases in which a decussate and dorsiventral shoot is gradually or suddenly transformed into a spiral and radial shoot. This happens especially when by some damage a leading branch loses its apex; one or more of its laterals may be transformed then in the indicated way [1]), rarely in the first, more frequently in the second, third or even a later year of their life.

Of such shoots I gradually succeeded in observing 12 specimens. In eight of them the leaf pairs, though remaining opposed and crossing rectangularly, showed such solutions as to constitute a leaf spiral with divergences of 180° and 90°; in some of these by the disappearing of the rectangular crossing a perfectly normal spiral was reached.

In the four remaining specimens the transition took place in a curious way, the same in all four; fig. 41 may illustrate this. It consisted of an unchanged arrangement of the leaf pairs situated in one of the two leaf planes (in the figure the pairs 1-2, 5-6 etc up to 53-54), whereas in the plane at right angles the slope of any two superposed pairs was in the reserve direction (from 27-28 upwards to 51-52).

The specimen represented in fig. 41 was drawn on account of the striking perseverance of this condition; in the other similar shoots this region was much shorter. A spiral condition was not reached in the drawn specimen, but it was in one of the three other cases.

On the basis of the simple explanation of the normal leaf arrangement by a shift of the leaves of the light side in the apical direction the specimen of fig. 41 has to be considered as a dorsiventral and decussate shoot in which the dorsiventrality and decussation becoming unsettled, the leaves of one of the two light side orthostichies continued to be shifted in the normal way, whereas in the perpendicular plane the shifts on the light side not only were left out, but even the whorl

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[1]) If my observations of these cases had been instituted after an intentional decapitation of the mother axis, they would perhaps have been deemed worthy by some botanists to be designated as belonging to experimental botany. As they have been simply made however on "nature experiments", this honour will not be allotted to them.

Herniaria incana, procumbent shoot system. For description see § 30.

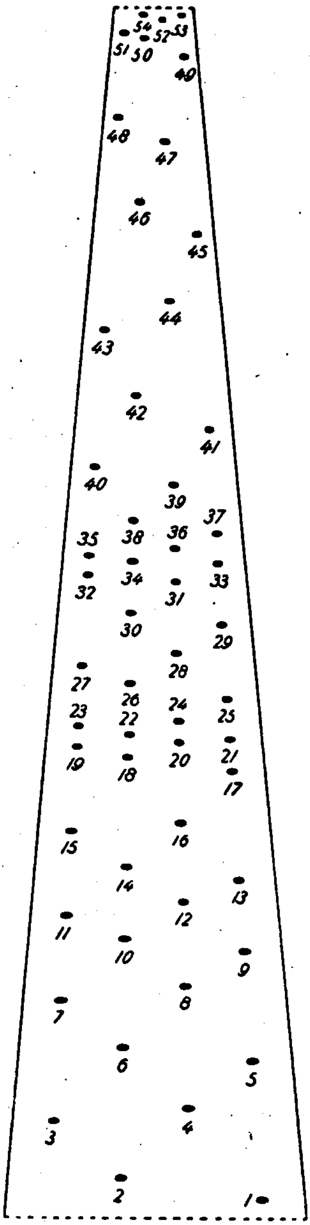

Fig. 41. *Rhamnus Frangula.* Surface of particular shoot, represented as telescoped and unrolled. Leaf insertions numbered according to insertion level. Height × 0.16; girth × 1.6; insertion levels true to scale. Middle orthostiches belonging to light side, outer orthostichies to shadow side; orthostichies supposed to be perfectly straight, which could not be controlled in the specimen. Leaf pairs 1—2, 5—6, etc up to 53—54 all dissolved by shifts in the normal way, the upper leaf being shifted in the apical direction. In the crossed pairs 3—4, 7—8, etc the same up to 27—28; all subsequent pairs with alternating slope direction, as a partial transition to a spiral arrangement.

formation was incomplete, the shifts for the levelling of the whorl members being omitted.

The obvious objection to this explanation is that it is not clear why the whorl forming should be less complete in one plane than in another.

In trying to follow out the *Paronychia* explanation for these cases we have to suppose that the difference between the dorsal and the ventral side of the apical meristem disappears in an asymmetrical way, remaining some time on the right or on the left side. If we make a theoretical construction like that of fig. 38 *A*, using the top of that figure as a base and adding dispersion circles with a radius of 0.45 in the white and of 0.25 in the hatched part, we find that if the hatched part is reduced to its right or left half as in fig. 42, we obtain a system which is comparable to that of the specimen of fig. 41 in every respect; the system may be continued in the same form ad infinitum and the pairs 11-12, 15-16, 19-20, 23-24 regularly alternate in their slopes, whereas the pairs 13-14, 17-18, 21-22, 25-26 all have the same slope.

The only fault of the theoretical construction is that one of the four orthostichies, that of the centres 13-17-21-25, follows a sinuous course. This might have been amended probably by more complicated suppositions, but it did not seem worth while to work this out.

Comparing fig. 38 *A* and fig. 42, we recognize that the line connecting the centres in the genetic order makes a turn at every centre following on a small circle; in fig 38 *A* this is at every third, in 42 at every fifth centre.

The conclusion to be drawn from these highly theoretical speculations in my opinion must be that the phyllotaxis of the dorsiventral shoots of *Rhamnus Frangula* may be simply a dorsiventral decussation with a shift of the leaves of the light side in the apical direction, but that it may just as well, and perhaps more likely, be an original zigzag arrangement, due to similar causes as described for *Paronychia*.

CHAPTER 7. DISCUSSION AND SUMMARY.

§ 34. The origin of binding whorls.

In a former paper (51) I demonstrated that, unless a plant has dichotomizing stems, leaf whorls in Cormophytes, when occurring regularly, not mixed with other forms of phyllotaxis, must be considered as false whorls arising by metatopies. For

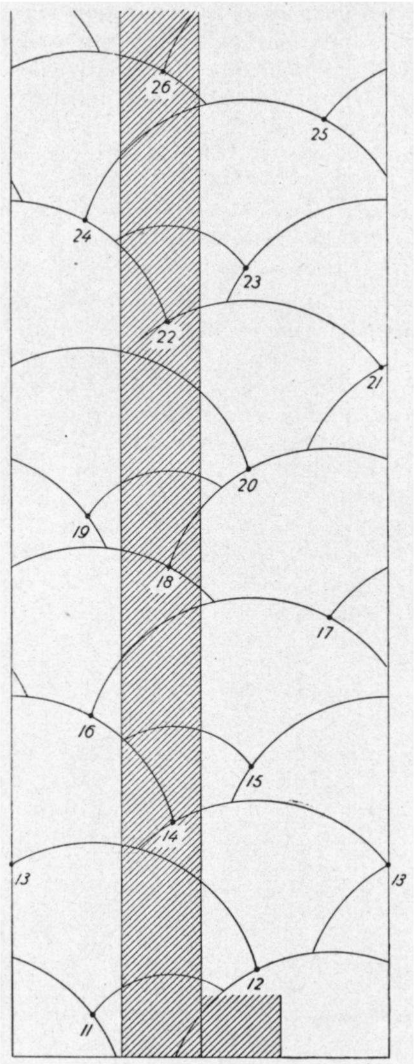

Fig. 42. Top of junction scheme of fig. 38 *A*, continued in the same way by adding dispersion circles, but with the difference that the longitudinal zone of smaller circles is discontinued unilaterally. Leaf centres now placed in a zigzag turning at every fifth centre.

foliage leaves these whorls are probably always binding whorls.

In the present paper a number of plant species, being nearly all Dicotyledons, with leaf whorls are described.

In plants with radial leaf whorls it was found that the original spiral is still recognizable in many cases.

The phyllotactical spiral, determined in such a way, is of the same description as that occurring in not whorled plants: in the overwhelming majority of cases it is a spiral with a divergence of about 135° to 144°. It was only in *Helianthus* that after special research some instances of whorls made from anomalous series could be detected; the majority of these cases belonged to the first accessory series.

The means by which the original spiral is to be recognized, are the insufficiencies or incompletenesses of the whorl formation; when in a shoot the spiral may be determined in more than one way, the results invariably confirm each other.

The morphological phenomena, described here as insufficiencies of the whorl formation, were well known to the botanists of the old idealistic morphological school, but as these botanists were inclined to take any arrangement as a consequence of eternal ideas they lacked the impulse for further research.

The botanists of modern times on the other hand had no knowledge of these phenomena, and so their significance has escaped attention up till now. Yet when put together and considered in due connection, the available facts fully establish the spiral origin of the whorls in many plant species with radial shoots.

In other plants with radially symmetrical whorls no traces of any spiral were found. But as these whorls must be false too, on the arguments adduced before, the most probable conclusion is that these whorls are binding whorls of the same origin as in the species of the former group, only they have been realized with such a degree of perfection as to leave no deficiencies of any kind.

In dorsiventral shoots the whorls being subject to the influence of the dorsiventrality factors, it is obvious that the chance of finding traces of the spiral is much lessened. Indeed the observed traces were scarce, and where present, they were weakly expressed.

Yet feeble traces, when undeniable, furnish proof that in these shoots the whorls are of the same make as in radial shoots, and only differ by the superposed influence of the dorsiventrality factors. Once so far it is only a step to extend the result to the other plant species with dorsiventral whorls, in which no trace of a spiral origin has been stated.

It is only in the case of some *Caryophyllaceae,* namely of *Herniaria* and *Paronychia,* and perhaps in that of *Rhamnus Frangula,* that we have reason to assume that the original phyllotactical pattern of the shoot is neither a spiral nor a whorled one, but that the genetic order of the leaves is a zigzag line, of the exact form as was postulated for all dorsiventral and decussate plants by the old idealistic morphological school.

On the basis of a junction theory this curious fact may be understood to a certain degree, by assuming that the dorsiventrality factors in the shoots of these species are active high up in the apex, even above the region in which the leaf centres are induced, as set forth in § 32.

§ 35. Taxonomic value of the difference between radial and dorsiventral binding whorls.

The occurrence of common hereditary factors in two organisms being an indication of a certain grade of relationship, any hereditary feature, observed in different species, is of some taxonomic importance.

As the binding whorls are of wide-spread occurrence in Dicotyledons, in the cotyledons, in the prophylls and moreover often in other kinds of phyllomes, they have to be considered as taxonomically important for the Dicotyledons; in the Monocotyledons they are nearly absent, though not quite (*Hydrilleae*), while in the Gymnosperms we have some striking instances of plant groups with binding whorls in all their leaves (*Cupressaceae, Gnetales*).

For the latter groups the importance has been duly recognized in botanical literature. For the Dicotyledons on the other hand we find sometimes instead of such a recognition a rather different point of view, namely that it is chiefly the contrast between the radial and the dorsiventral decussation which has a taxonomic value.

This is foreshadowed already in SCHIMPER's *Symphytum,* when he opposes the phyllotaxis of „Caryophylleen, Gentianen und andere" (45, p. 86) to that of *Salix purpurea, Fraxinus,* etc; it is silently assumed by WICHURA (66, p. 181), by HOFMEISTER (28, p. 471, 472) and by SCHWENDENER (54, p. 82) and it has been enounced in a very striking way by DELPINO (16, p. 247) who even went so far as to deny a radial decussation in the

Caryophyllaceae, Asclepiadaceae and *Acerinaceae,* as these groups were too much akin to the *Salsolaceae,* the *Apocynaceae* and the *Rhamnaceae.*

This negation of evident facts, in order to keep up a theoretical conception, has already been duly criticized by WYDLER (84), who remarked that both forms of decussation may occur in the same group; as instances he quotes the *Acanthaceae,* the *Lythraceae,* and the genus *Veronica.*

On closer examination we recognize that radial and dorsiventral decussation essentially are not two opposed features, dorsiventrality being an elaboration of radial decussation by the addition of dorsiventrality.

If really the two forms had been independent acquisitions of the form-giving powers in the plant, as for instance foliar and ramular tendrils, their occurrence might have had taxonomic importance. But any plant with dorsiventral decussation can return to radial decussation by the inactivation or by the loss of the dorsiventrality factors, just as any plant with dorsiventral flowers can form peloria or can produce a variety with radial flowers.

So our conclusion may be that while the occurrence of binding whorls has a taxonomic value, the contrast between radial and dorsiventral binding whorls is not of the same description.

§ 36. **Summary.**

1. A certain number of plant groups with early binding whorls are described. The special results for the particular cases having been dealt with in special paragraphs to which the reader may be referred, the following general results may be mentioned.

2. The early binding whorls in several cases show traces of the original phyllotactical pattern. In the examined cases this pattern almost without exception was a spiral system of the main series, with a divergence between 135° and 144°.

As rare exceptions deviating shoots may be found with systems from other phyllotactical series; in an extensive culture of *Helianthus annuus* these exceptions were collected and investigated. They belonged in majority to the first accessory series, some of them to the first jugate series and a very few to the second accessory series.

A real exception to these rules was found in the genera *Paronychia* and *Herniaria,* where from the phenomena of the calyx aestivation of the terminal flower it was deduced that the original system in all shoots is a zigzag line, not a spiral; in *Rhamnus Frangula* the same zigzag is perhaps present.

3. Binding whorls may occur in a radial and in a dorsiventral form. The radial form being primitive, the dorsiventral form is essentially similar but for the supplementary action of dorsiventrality factors, altering the binding whorls to a larger or smaller extent.

As these dorsiventrality factors may be lost or may be inactivated, a species with dorsiventral binding whorls may produce a variety with radial binding whorls, and an individual plant with dorsiventral binding whorls may even produce shoots with radial binding whorls. Accordingly the contrast between the two forms has little taxonomic value.

4. For the elaboration of perfect binding whorls the following processes are required: the establishment of the lateral binding into a whorl, the levelling of the whorl members, the equalization of the angles between them, the adaptation of the successive whorls to a certain form of junction, being nearly always alternation, and the elimination of the age differences between the members.

These processes may all be executed with a greater or smaller degree of perfection.

5. In consequence of the binding process nearly always whorls are formed.

In exceptional cases the binding does not close around the apex, so that partial whorls ensue, as illustrated by fig. 30-32.

A more important anomaly is the formation of a secondary spiral instead of whorls, when one end of a horizontal leaf row joins up with a leaf situated above the last leaf of the other end; the binding is then continued in coils winding round the apex.

The fact that most plants with binding whorls may produce shoots with biastrepsis as rare exceptions is to be explained in this way.

When the successive coils of this secondary spiral are adapted to alternation of the constituent leaves, the secondary pattern assumes the form $m + (m+1)$.

6. In shoots with biastrepsis the secondary phyllotactical pattern may be determined by the observation of the decurrent fibres from the leaves in the stem.

In species where the normal shoots are decussate this secondary pattern, as far as our record goes, is always $2 + 3$. This is a proof that in such shoots the original system has been of the main series and that the binding has occurred along the SW genetic spiral.

In species with polymerous whorls the secondary patterns are 3 + 4, 4 + 5, etc; in many cases however the formulae are less distinctly realized, as the alternation of the successive coils is imperfect, just as the alternation in the polymerous whorls of the normal shoots is.

7. In such cases where either the levelling of the whorl members, or the equalization of the angles between them, or the elimination of the age differences, is not executed to the full, traces of the original phyllotactical system remain.

These traces must be distributed in a regular way in the successive whorls, a way which only depends upon the whorl numbers and upon the original system.

In systems of the main series alternating dimerous whorls must have a distribution of the peculiar features in antidromous ¼ spirals, alternating trimerous whorls in homodromous 1/6 spirals, alternating tetramerous whorls in antidromous 3/8 spirals, alternating pentamerous whorls in antidromous 1/10 spirals; in the first accessory series alternating trimerous whorls have their peculiar features in antidromous 1/6 spirals, alternating tetramerous whorls in homodromous 1/8 spirals, etc.

These deductions have been fully confirmed by the observation; for the anomalous series see especially § 24.

8. A comparison of the degree of perfection of the adult whorls and that of homologous whorls in the developmental stages shows that the whorl formation processes may have already been carried to completion at the moment in which the primordia begin to bulge out.

In other cases they are only partially completed at that moment, so that the remainder has to take place during the visible developmental stages.

In a few cases where the transverse metatopies are completed at the moment of bulging out, it is possible to show that the required transverse shifts really have taken place during the invisible stages, by the fact that the median leaf traces only correspond to the shifted insertion place in the upper half of their downward course in the stem, the lower half corresponding to the original insertion places.

This is due to the circumstance that the induction of the leaf trace course having taken place during the invisible stages, only the upper half could be shifted with the prospective primordium, whereas the lower half which runs in the domain of other leaf insertions, had to remain in its place.

9. The differences in age of the whorls members, whether eliminated very early or not, of course leave no traces in the adult condition.

In a number of species however the axillary buds of different developmental stages, being exposed simultaneously to the morphogenetic forces in the whorl, react differently, so that their development may follow different paths.

The difference may only pertain to their vigour, in which case in some plant groups the older, in others the younger buds are furthered, or it may entail a wholly different kind of plastics.

In any case the buds of the same kind are distributed in the successive whorls according to the rules indicated sub 7.

10. The formation of binding whorls often forming part of the plastics of only a certain leaf category, other regions of the same shoot may be free from binding. In such cases the original pattern may be traced from the not-whorled into the whorled part and the original order of the whorled leaves may be determined.

Shoots, with binding whorls in their lower region only, may have a sudden transition to the not-whorled region (discontinued whorls) or a gradual transition (dissolving whorls).

In the former case odd leaves may be left between the whorls and the higher region, in such places as are required by the phyllotaxis of that higher region; in the latter case the transitional region may be particularly instructive through its numerous insufficiences in the whorl formation.

11. In the numerous cases in which the original phyllotaxis of a shoot with binding whorls could be determined in two or more ways, the outcome of these different methods was identical, without any exception.

12. Lateral connation of phyllomes, being only freely possible in false whorls, occurs in some plant groups with binding whorls, as in *Equisetum.* If biastrepsis occurs in shoots of such plants, the connation is an additional difficulty for the elongation of the shoot.

13. The explanations, previously given in literature for the origin and the peculiar features of binding whorls and for the existence of bud spirals in the same shoots, based on the principle of rhytm, or on junction phenomena in true whorls, are reviewed and discussed; they are all found to be contra-

dictory to the facts, with the only exception of the explanation given by RACIBORSKI for the bud distribution in *Cupressus*.

A consideration of the facts to be observed in *Cupressus* shows that really the case is different from that in Dicotyledons in so far as a sterile whorl between two bud-bearing whorls does not count in *Cupressus*. RACIBORSKI's suggestion that the bud distribution in *Cupressus* is a true cladotaxis, is therefore to be accepted, whereas in the Dicotyledons it is wholly based on phyllotactical processes.

14. In dorsiventral binding whorls the spatial relations between the phyllotaxis and the dorsiventrality factors are usually fixed, at least when the dorsiventrality is clearly pronounced.

This relation in dorsiventral decussation amounts nearly always to a diagonal position of the four orthostichies with respect to the ventral and the dorsal sides; in a few plant groups the ventral and the dorsal sides coincide with two of the orthostichies, the other two being lateral.

In rare instances the spatial relations may be subject to anomalies or shifts.

15. Under the influence of the dorsiventrality factors a number of special features may arise.

The leaves may shift in the longitudinal sense, those at the light side often shifting in the apical direction.

The leaves may shift in the transverse sense, often all leaves approaching the dorsal median line.

The leaves on the ventral and those on the dorsal side may develop differently (anisophylly), the light side leaves often being smaller, sometimes even rudimentary or aborted.

The right and left side of individual leaves may develop differently (inequilaterality).

The buds on the dorsal and on the ventral side may get different plastics.

In diagonally dorsiventral decussation all similar organs are placed in a zigzag line on the ventral or on the dorsal side.

16. In dorsiventral binding whorls the traces of the original phyllotaxis have usually disappeared.

In some species with weakly expressed dorsiventrality such traces may still be present (*Epilobium montanum*); in other species the dorsiventral whorls being discontinued, a spiral comes to light (*Helianthemum apenninum*).

17. The strange fact that the original phyllotaxis of the dorsiventral shoots of *Herniaria* and *Paronychia* seems to be

a zigzag arrangement, as judged by the calyx aestivation of the terminal flower, a condition which perhaps may also be realized in *Rhamnus Frangula,* has given rise to the following consideration.

If in the shoots of these genera the dorsiventrality factors are active at an unusually high level in the apex, above the region in which the leaf centres are induced, and if by the influence of these factors the dispersion circles at the dorsal side are markedly reduced, the leaf arrangement indeed may become a zigzag, turning at every third leaf.

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