ON WHORLED PHYLLOTAXIS.
III. TRUE AND FALSE WHORLS [1]

by

J. C. SCHOUTE.

§ 1. The distinction between true and false whorls.

As already pointed out earlier (19, p. 186), in the literature on phyllotaxis relatively small attention has been paid to the whorled systems, the interest usually being centered in the explanation of the curious divergence phenomena of the spiral systems.

Yet the notion of false whorls is as old as the doctrine of phyllotaxis itself; Brongniart in 1828 wrote about „des verticilles floraux [qui] ne sont pas réellement verticillés" (7, p. 226), and Schimper wrote in 1829 that whorls in which the leaves are inserted around a single node do not exist, all leaf whorls having a definite succession of their members (17, p. 85).

A definition of true and false whorls as far as I know has not been given in the century elapsed since, and the way to distinguish between them has never been indicated.

In the present paper whorls will be called true when the position of the members has been determined in such a pattern that there are two sets of antidromous contact parastichies with equal coordination numbers; in other words when the system has been induced as an m+m pattern. False whorls will be those systems which have been laid down in the form m+n, with unequal numbers of contact parastichies but where, by subsequent processes, the adult condition has assumed a whorled appearance.

For true whorls it is therefore not required that the members of one whorl are inserted at the same level or at the same distances; for the horizontal distances the limits may be indicated according to my phyllotactical theory as lying between 1 and 1.7 times the radius of the dispersion circles (18).

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[1] For I and II see literature 19 and 20; a fourth paper on „Early binding whorls" is in preparation. On the present topic a preliminary communication was read in the meeting of the Nederlandsche Botanische Vereeniging on Jan. 22nd 1923, see Nederl. Kruidk. Archief, jaargang 1923, 1924, p. 46.

These definitions are based in the first place on the fundamental theorems established by the Bravais' (5, p. 45-58), and further on the consideration that no natural phyllotactical system will ever be mathematically regular, but that it is practically regular, as soon as the parastichies can be counted (18, p. 195).

The same definitions were inexplicitly held by Hofmeister (12, p. 500) and by Schwendener (22, p. 55). Other authors, taking symmetry as a governing principle in plant construction, require accurate equidistancy and exactly the same level for whorl members; this point of view is explicitly taken by Church (8, p. 142). Still other views are held by those authors who try to solve morphological problems from a phylogenetic starting point; Zimmermann may be quoted as the most consequent promoter of this method (34).

According to Zimmermann the fact that morphologists generally disagree on the nature of the relation between spiral and whorled phyllotaxis is due to the lack of a phylogenetical basis for their investigations (34, p. 241). The phyllotaxis of the ancestors is taken by Zimmermann to represent the phylogenetical starting point for the different systems of the progeny; by a shortening of the internodes and a change in the divergence angles an ancestral spiral may turn into a whorled phyllotaxis. Intermediate stages in recent plants are the material from which conclusions may be drawn about the progressive course of this development (p. 319). From this view point the difference between true and false whorls disappears altogether (p. 241).

In my opinion the whole conception is not acceptable. Of course the knowledge of phylogenetical evolution, if available, might be extremely helpful in the solution of morphological problems. But we have to bear in mind that no less an authority than D. H. Scott towards the end of his life once said in a discussion (23, p. 39): „The rejection of phylogeny by some modern morphologists is, in a sense, justified. We can infer nothing from phylogeny, because phylogeny is unknown, 'a product of fantastic speculations' as Lotsy called it. To infer morphology from phylogeny is to put the cart before the horse".

In this special case we may be sure, that even if Scott's wise words had not already settled the question, Zimmermann's view could not have even a partial correctness for the following reason. The idea that a phyllotaxis is inherited as such, demands, as Zimmermann is obliged to admit (34, p. 321) that there are elementary processes for the regulation of the length of internodes and others for the divergence angles. Now it is not difficult to show that neither the length of internodes nor the size of the divergence angles are subject to a direct regulation by hereditary processes, both being the casual results of the spatial relations between the leaves.

The growth in length of any stem to a large extent no doubt is regulated by special genes; in stems of the same plant with different plastics this regulation may differ considerably through the activity of different genes. But this growth is general growth, not growth of separate internodes. In a plant which usually bears its inflorescences on leafless scapes, we may often find some stems with one single leaf or bract midway on the scape, so that the latter instead of consisting of one single internode is formed of two shorter internodes. But the total length is not changed.

In the same way the divergence. When in a Lycopod a 4+5 system with a 2/9 divergence changes into a 5+5 system with no divergence at all, this is not due to a sudden change in the action of the divergence genes, but only to a slight difference in the spatial relations at the stem apex.

The retrieval of morphology by Zimmermann will therefore perhaps not be equally appreciated everywhere in the morphological camp.

The last author on the topic I have to quote is Goebel, who wrote in 1913 (11, p. 72) that false whorls are imitations of true whorls, and that, as the imitation may develop into a real correspondence, a striking contrast between the two categories was not to be assumed. These views and the arguments upon which they are based not being clear to the present writer, a discussion of them may be withheld.

So the above definitions of true and false whorls may provide us with a basis. Our next task now is to investigate how such true and false whorls, if realized in nature, may be distinguished.

In the first place we understand that the mode of variation must be different. When the spatial relations at the stem apex change and consequently the system of contact parastichies is modified, the new systems arising above true whorls may perhaps be whorled again, but they usually will be either spiral or jugate or wholly irregular (18, p. 257). In these new systems of course metatopies might occur, changing the system into false whorls. But even this is not probable, as the required morphogenetical forces, if absent in the lower whorled part, are not likely to be suddenly present in the non-whorled higher stem part. And as will be dealt with below, biastrepsis is not to be expected in these cases.

Plants with false whorls on the other hand, on the changing of the original phyllotactical pattern, still keep the same morphogenetical forces for false whorl formation, and the new phyllotactical pattern therefore will be transformed into false whorls all the same.

Now it is well known, and instances will be given in number below, that plants with false whorls may also vary with spiral systems. At first sight this fact might seem contradictory to our views. A closer investigation however reveals that this is not the case.

The cases of spiral systems in otherwise falsely whorled plants may be divided into two wholly different categories.

In the first place we have those where the false whorl formation is only specific to a certain region of the shoot, for instance to the region of the foliage leaves, and where the bracts are not whorled. In a terminal inflorescence the whorl formation factors of the lower foliage leaves will then be inactivated at the transition from leaves to bracts. And as this transition often is a gradual one, the inactivation of the false whorl factors may be gradual too.

It is clear that such cases, if obtaining in a general way in regions of definite plastics, offer no objection to our views, but rather are an indication that false whorl formation in these plants is part of the shoot plastics itself.

The other group of spiral systems is that where, in exceptional cases, spirals are to be observed in those stem parts which in the same species, and usually in the same plant in other stems, are whorled.

When this occurs in plants with growth whorls, where the whorled appearance is only due to a very unequal distribution of the growth in length over the shoot, some transverse zones of the stem undergoing an excessive elongation (19, p. 194), the return to the spiral phyllotaxis may evidently be brought about by a more equal distribution of the growth in length. This has for instance been described by Kros (14, p. 95) in *Lilium Martagon* ²).

When on the other hand the spiral systems occur in plants with

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²) When in 1922 I described L. Martagon as a typical instance of growth whorls, I was unaware of the fact that this clear case of false whorl formation had already captured the attention of several predecessors.

In the second paper of this series (20, p. 130) I have mentioned the description by the Bravais'; now I can add that Wydler gave a very detailed description (30, p. 36) and that he moreover in the same paper pointed out clear cases of growth whorls in *Pastinaca, Heracleum, Aegopodium* and *Chaerophyllum*, cases comparable to those I found in *Ferula thyrsiflora*. Lastly Velenovsky (24, p. 570) also mentions the false whorls of *Lilium Martagon* and some other *L.* spp.

binding whorls, it is easy to show that in nearly all cases the spiral system is not due to a lack of the false whorl forming factors, not to an inactivation of the binding therefore, but to a binding in an unusual way.

When the binding, instead of uniting the collateral organs into a ring, on being started at one side of the stem does not close up at the opposed side, but its one end unites with a row of organs lying over those to which the other end leads, a winding spiral is initiated which further on may continue uninterruptedly. This winding spiral may be identical to the original leaf spiral, when the primordia unite after the SW (= short way) or the LW genetic spiral. It may however be any other spiral, made up of parts of different kinds of parastichies.

The results of such abnormal spiral bindings may be rather different according to growth conditions in the shoot. When there is a marked growth in length of the stem, and the binding is firm enough, either by connation of the leaves or by coherence of their insertions, the stem on elongating will have to surmount the resistance of the spiral leaf band, and will be twisted itself in the opposite direction.

This phenomenon is well known through the short, but splendid exposition of facts by Al. Braun (3, p. 440, or p. 10 of the reprint), under the name [3]) biastrepsis (Zwangsdrehung). Braun fully explained the whole process and its consequences. The only essential addition to the theoretical elaboration of his views was made later on by de Vries (26), who succeeded in showing experimentally that if the coherence in the winding spiral is broken artificially, the torsion of the stem is locally absent.

Braun and his followers were obliged to admit that the sudden change from whorled to spiral phyllotaxis was an independent phenomenon, not related to the whorl formation itself. The above explanation, by adding the conception that both whorls and abnormal spiral are due to the same binding forces, increases the unity of the phenomena.

When there is only a very slight growth in length all torsion of course is absent; this again was fully realized by Braun and instances were given (4, col. 31) in which this was the case (*Pycnophyllum*, binding after SW genetic spiral; *Crocus* spp,

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[3]) About the nomenclature of these phenomena confer de Vries (26, p. 81): The term biastrepsis may namely be used in a wide sense, including all kinds of plant torsions (C. Schimper) or in a narrow sense as an equivalent of the German Zwangsdrehung or the Dutch klemdraai (Braun). The latter use will be followed here.

coalescence after LW genetic spiral); the same was confirmed by de Vries (26, p. 125, *Dipsacus*, radical rosette and elongated stem).

In the second place we have to investigate whether a difference may be expected between true and false whorls in the occurrence of two-topped leaves.

These abnormal leaves may arise in two wholly different ways. In the first place by dichotomizing of the leaf apex. This faculty of dichotomizing is present in the leaves of some Ferns (for instance in *Scolopendrium officinarum)* and in some Pteridosperms (for instance in *Lyginodendron oldhamium),* in plants therefore whose leaves are still near to the original branch system condition from which the macrophylls are believed to have been derived.

In the Angiosperms this dichotomizing faculty to all appearance has been lost. Yet two-topped leaves are found in these plants too, and here it is well known that their frequency is related to the phyllotactical pattern. Delpino showed namely that their frequency is very small in regular spiral phyllotaxis (9, p. 226) but relatively much higher in irregular systems and in whorled plants (p. 202). As I tried to demonstrate on an earlier occasion (18, p. 185, 242) this form of two-topped leaf is due to connation, and it may arise when two leaf centres are induced in an unusually close proximity; if this supposition be correct it is clear that the relatively high frequency in irregular phyllotaxis is quite natural.

For true whorls, which on change of phyllotactical pattern usually will become irregular, an increased frequency of connations may equally be expected; for false whorls arising from a main series pattern this might on the contrary seem not to be the case. Yet the occurrence of two-topped leaves in evidently falsely whorled plants is so common, as we shall see below, that there must be some other explanation.

When we consider the cases in which two-topped leaves are to be observed in plants with false whorls, we soon recognize that the two-topped leaves usually occur on the transition places between whorls of different leaf number. In such cases it is evidently not the origin of two leaf centres in an unusually close proximity which is the cause of the connation, but the two leaf primordia being crowded together at a somewhat later stage under the influence of an adaptation of the heteromerous whorls to alternation.

Delpino pictures for instance two branches of *Aloysia citriodora* (9, pl. 11, fig. 70, 71), the first having four whorls of 4, 4, 3, 3 and the second three whorls of 3, 4, 3 leaves. The second whorl in both has two of its leaves fused. Evidently the whorl of four leaves, in becoming alternate to the trimerous whorls, has had two of its leaves crowded together and fused.

It will be obvious that if this explanation be correct, the two-topped leaves are to be expected in binding whorls only, not in growth whorls.

Summarizing we may say that true whorls will never be found dominating, but always in a varying state with other systems; they may not give rise to biastrepsis, but two-topped leaves may occur in them. False whorls on the other hand must always occur in a dominating position. They may occur all over the plant, or they may be limited to certain leaf categories, leaves of other plastics being free from them.

Biastrepsis may occur in binding whorls only, not in growth whorls, and two-topped leaves may occur in growth whorls only when the original phyllotaxis is irregular.

§ 2. The distribution of true and false whorls in vascular plants.

A. False whorls.

From the considerations in our first § it will be clear that false whorls will be more frequent than true whorls in vascular plants. Particularly those plant groups which usually have been considered as the best examples for whorled phyllotaxis, as they never show other than whorled systems, are now heavily suspected of having false whorls; some of these groups will be discussed here in the first place.

1. The *Articulatae.* In the Articulatae the whorled condition is to be found in all parts of the shoot; rhizome, aerial vegetative shoot and strobilus. The consecutive whorls of a shoot usually are heteromerous; the junction of one whorl to the lower whorl in most groups is alternate, as much as may be consistent with the heteromery (for details see 25, p. 39). In a few groups the junction is superposed, a mode of junction which must be considered entirely impossible in true whorls.

For *Equisetum* biastrepsis has often been observed (Penzig 15 III, p. 564); other spiral systems are not known.

All this proves that the whorls are binding whorls.

2. *Cupressaceae.* The foliage leaves and the sporophylls always occur in whorls, usually in dimerous or trimerous, sometimes in tetramerous whorls; the whorl number may sometimes vary in the course of the shoot, and in trimerous whorls this is always the case at the base, as every branch begins with a lateral dimerous

whorl. Spiral systems or biastrepsis are not reported in Penzig (15 III, p. 510—515).

Cases of two-topped leaves have not come to my notice. In *Juniperus communis* in 25 branches with a transition from di- to trimerous whorls I did not find one.

The whorls evidently are binding whorls.

3. *Gnetales.* The leaves and sporophylls are always whorled; they occur in dimerous, sometimes in trimerous, rarely in tetramerous whorls. Biastrepsis seems not to have been reported.

In *Ephedra distachya* I observed numerous lateral branches beginning with one, up to three, decussate pairs, followed by trimerous whorls; in only one instance had the first trimerous whorl two of its leaves united into a two-topped leaf.

Conclusion: binding whorls.

4. *Hydrilleae.* The foliage leaves occur in whorls, according to Engler & Prantl, (10, II, 1, 1899, p. 250) the whorl numbers being 2—8 for *Hydrilla,* 2—9 for *Elodea.* In *Elodea canadensis* and *E. densa* every lateral shoot begins with some, often with four, decussate pairs, after which trimerous whorls follow without any transition.

Biastrepsis is not mentioned in Penzig (15 III, p. 254), and from the secondary displacements of some leaves to other whorls, in the mode of growth whorls (19, p. 204), their occurrence is not very probable, as the binding evidently easily yields.

Conclusion: binding whorls, sometimes complicated by secondary phenomena reminding one of growth whorls.

5. *Casuarinaceae.* The foliage leaves invariably are arranged in whorls, from 2 up to 12 leaves in a whorl. Lateral branches always begin with a lateral dimerous whorl; whorls of higher number follow without any transition. Our fig. 1 represents the first three whorls of a branch of *C. stricta.*

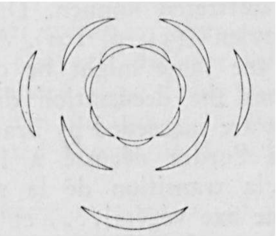

Fig. 1. *Casuarina stricta,* diagram of particular case of branch base.

Biastrepsis has often been observed (Penzig 15 III, p. 475). In C. *sumatrana* I observed that when a diagonal tetramerous whorl follows on a dimerous whorl, the usual condition at the branch bases, the two posterior leaves of that tetramerous whorl are sometimes connected up to their apices, so as to form a triangular complex with two midribs.

Conclusion: a clear case of binding whorls.

6. *Hippuris.* The foliage leaves are whorled; heteromery often occurs. In a particular shoot for instance the higher part showed the following sequence: 9, 9, 9, 9, 9, 10, 11, 10, 11, 11, 11, 10, 10. The branch base always is strongly heteromerous; in 26 lateral shoots the first whorl invariably was dimerous; the second whorl once dimerous, 19 times trimerous, 5 times tetramerous, once pentamerous. The third whorl was hardly related in number to the second: 4 times trimerous over a trimerous second whorl; 10 times tetramerous (8 over 3, 2 over 4); 11 times pentamerous (once over 2, 7 times over 3, twice over 4, once over 5) and once hexamerous over a tetramerous second whorl.

Biastrepsis has often been observed (Penzig 15 II, p. 362); connate leaves seem to be lacking altogether.

A clear case of binding whorls.

7. *Labiatae.* The leaves and bracts nearly always are strictly decussate; yet in many species specimens with „folia terna" have been observed, often with two-topped leaves (Penzig 15 III, p. 144) and biastrepsis is wide-spread (ibid. p. 143). Some genera have typically trimerous up to octomerous whorls (Engler & Prantl 10, IV, 3a, 1897, p. 186).

Without any doubt the whorls are binding whorls.

8. *Other dicotyledonous decussate plants.* In probably all of them trimerous whorls occur in exceptional cases; numerous examples have been recorded by Schimper (17, p. 107), and Wydler even writes: „Man kann im Allgemeinen für alle mit foliis oppositis versehenen Pflanzen als Regel annehmen, dass sie auch mit foliis ternis auftreten können. Dies gilt auch von den Keimblättern der Dicotylen" (33, p. 201). And about two-topped leaves and biastrepsis the same might be contended.

In many Dicotyledons the decussation disappears at the level where the foliage leaves are succeeded by bracts; as the Bravais' wrote: „le passage de l'ordre décussé à l'ordre alterne.... se présente souvent dans la transition de la partie végétative à la partie florale d'un même axe végétal.... et pour prouver combien le voisinage de la fleur tend à faire prédominer l'ordre alterne, nous citerons ici le fait de la tige décussée du *Melaleuca hyperici-*

folia qui devient alterne curvivisériée à l'épi floral et se prolonge, l'année d'après, en une tige foliacée décussée" (6, p. 212); another example of the same phenomenon has been described by Weddell for several *Urticaceae* (28, p. 12), when the inflorescence axis with its spiral bracts grows out into a decussate leafy shoot, as regularly occurs in *Boehmeria cylindrica* var. *phyllostachya* (28, pl. 11, fig. 18).

In other Dicotyledons the decussation disappears somewhere midway through the foliage leaves *(Helianthus Nuttalii, H. parviflorus, H. strumosus,* all becoming spiral about at the level where the lateral branches begin) or still earlier, so that after the cotyledons only a few or even no decussate leaf pairs are formed. As Wydler writes: „wie man.... in Hunderten von Fällen findet, wo entweder auf die paarigen Cotyledonen sogleich krummreihige Stellung folgt, oder erst nach einer grössern Anzahl von Blattpaaren, wie bei *Scrofularia, Veronica, Verbena,* etc." (31, p. 315). And on another occasion: „Nur die wenigsten Dicotylen lassen auf die Kotyledonen sogleich eine höhere Spiralstellung eintreten, sondern es folgen auf die Kotyledonen meist noch eine kleinere oder grössere Zahl von Blattpaaren, welche sich dann oft vor Beginn der Spiralstellung auflösen, aber noch mit Beibehaltung der rechtwinkeligen Decussation" (32, p. 358).

A somewhat different distribution of decussate and spiral phyllotaxis is to be observed in the genus *Catha* (Raciborski, 16, p. 21, fig. 9: *Catha emarginata;* own observation: material from Buitenzorg of *C. edulis)* in which the long main axes have a normal spiral phyllotaxis, and the laterals though having similar leaves are decussate shoots, with a limited number of leaf pairs, often three.

So these dicotyledonous decussate whorls evidently are binding whorls, restricted to one or more leaf categories.

9. *Cotyledons of Dicotyledons.* The arrangement of the cotyledons usually is considered to represent a true dimerous whorl; Zimmermann however is inclined (34, p. 280) to take it as derived from an ancestral spiral arrangement by a phylogenetical change. In view of the above it becomes tempting to take it as a binding whorl, and indeed some facts point in that direction.

In the first place we have the fact of the wide-spread occurrence of tricotyls, already quoted above sub 8 as having been reported by Wydler.

The phyllotaxis following on a whorl of three cotyledons may be an alternating trimerous whorl pattern. But, as is remarked by de Vries, the man who probably saw more polycotyls than any other botanist before or after him, this only happens in plants which otherwise are decussate (27, p. 229). In other terms: The trimerous whorled condition of the cotyledons is transmitted to the plumular leaves only when the binding factors are present in the latter.

This is a strong argument for the view that the cotyledonary whorl itself is a binding whorl too. For if it were a true whorl, its pattern should be transmitted in all cases, unless the spatial relations at the apex should cause a change of parastichy numbers.

Hofmeister mentions (12, p. 499) that the two cotyledons often are not strictly opposed, but more or less closer together on one side. This fact is even the chief argument on which Zimmermann bases his phylogenetical view. To my opinion however this fact, though undoubtedly correct, does not furnish us with any proof of a spiral origin, as the larger space at one side may represent a spatial adaptation to the development of the first plumule leaf which invariably falls in that space.

But there is a better proof in the *Stellatae* when the two cotyledons show an approaching together in the same way as all subsequent leaf pairs, so that the smaller angles of cotyledons and leaf pairs ascend according to a ¼ spiral, as will be dealt with in the next paper of this series. For this enables us to discriminate between the first and the second cotyledon and to show that the leaf spiral runs uninterruptedly from the first to the second cotyledon and so on through the foliage leaves.

In *Calandrinia grandiflora* I observed another clear case. The leaves following on the cotyledons, being arranged in a spiral phyllotaxis, regularly increase in size with their number in the leaf spiral. The two cotyledons which have the same plastics as the plumular leaves, always differ somewhat in size, in such a way that the cotyledon which takes the first place in the spiral is smaller; the lengths of cotyledon 1 and 2 in four arbitrarily chosen seedlings were 8 and 9, 7 and 10, 7 and 9 and 5 and 9 mm.

A further fact to be considered is the occurrence of connate cotyledons: the syncotyls, hemitricotyls, hemitetracotyls etc. Above, the two-topped leaves in Angiosperms have been taken to arise either by induction of two leaf centres in an unusually close proximity, or by adaptation to alternation in heteromerous binding whorls.

In part of the abnormal seedlings the latter explanation no doubt may hold true. One might suppose that through lack of a lower whorl an adaptation in number of the cotyledonary whorl might be out of question.

This however is not so. In the cases, described by Delpino for two-topped leaves in foliage leaves, we have full proof that a two-topped leaf may be due to the influence of the next higher whorl. Delpino distinguished (9, p. 220) between „sdoppiamenti positivi" (e.g. 3, 3½, 4), „sdoppiamenti negativi" (4, 3½, 3) and „sdoppiamenti neutri" (3, 3½, 3). In the positive doubling the connation evidently is due to the leaf distribution in the next lower whorl, but in the negative it is the higher whorl which conditions the fusion of two leaves; the latter case may be paralleled in the connate cotyledons.

Of course in cotyledons many irregularities may be present, causing connations in various way. Yet it seems to be a fact, as far as can be made out from literature [4]), that hemitricotyls at least usually have a dimerous first plumular whorl, tricotyls usually a trimerous; the hemitricotyls therefore in these cases may owe their connation to the fact that two of their cotyledons have been crowded together by the dimerous plumular whorl.

10. *Prophylls of Dicotyledons.* If the dimerous cotyledonary whorls be binding whorls, the same of course might be inferred for the prophyll whorls. Now it is well known that prophylls are often inserted at different levels, and moreover that they often converge, either to the back or to the front side of the shoot. Usually these departures from the regular dimerous whorl are such as to initiate the spiral of the subsequent phyllomes. For examples the numerous flowers with α and β converging at the posterior side and with sep. 1 at the anterior side, nearer to β, may be quoted.

Accordingly the Bravais brothers treat these prophylls as „des feuilles géminées", as being „réellement alternes, quoique verticillées en apparence" (5, p. 80, 81).

Moreover we have the remarkable fact, reported by Wydler (32, p. 357), that the mode of junction of spiral systems to the highest leaf pair of a decussate system is absolutely the same as that to cotyledons or to prophylls or to a distichous phyllotaxis. This points out again that all these main series systems essentially are congenial.

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[4]) Holden and Bexon (13, p. 518): in 9 hemitricotyls of *Cheiranthus Cheiri* two epicotyledonary leaves in 8 cases; in 32 tricotyls three in 31 cases; Bexon (1, p. 85) in 38 tricotyls of *Centranthus ruber* three epicotyledonary leaves in 35 cases, in 39 hemitricotyls the condition of the first plumular whorl was not mentioned; the three figures 2, 3, 4 of such seedlings showed only cases of a dimerous whorl; Bexon and Wood (2, p. 300): in 13 hemitricotyls of *Impatiens Roylei* two epicotyledonary leaves in 12 cases

11. *Floral whorls.* That in Dicotyledons the whorls of the perianth are false whorls has been extensively dealt with earlier (21); for the perianth of Monocotyledons no doubt the same holds true. The kind of whorls, whether they are binding or growth or still other whorls, may be left out of consideration here.

For the whorls of the sporophylls the mode of variation clearly shows that these too must be false.

B. True whorls.

Thus far our survey has taught us that in vascular plants the great majority of all whorls must be false whorls, and that amongst the false whorls binding whorls play a preponderant rôle.

The question may now be raised whether any true whorls are still to be found. As we shall see the answer must be in the affirmative.

For the realization of true whorls, in some way or other a number of leaf centres must be induced around the stem apex in the required places. Our fig. 2 represents a regular 4+4 system; the third whorl by its dispersion circles determines the place of the members a, a of the fourth whorl. Even when irregularities are present up to a certain extent, the resulting system will be truly whorled. The chance that the basal whorl of such a system will be realized incidentally, evidently decreases with the number of leaves in the whorl.

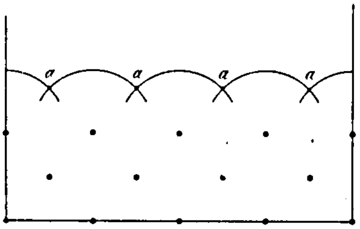

Fig. 2. Diagram of regular whorled system 4+4; *a, a,* centres of dispersion circles of next whorl.

In most vascular plants the phyllotaxis of any shoot is built up from a small beginning, the parastichy numbers at the shoot base being very low. These initial systems in the great majority of cases are spiral, as these have the lowest numbers.

In rising phyllotaxis any spiral or jugate system may gradually change without loss of regularity into the next higher system of the same series. The chance that a whorled system will change into the next higher system of its series, for instance 4+4 into 4+8 is very small; usually a whorled system will become irregular; and a whorled system will never result from it in a regular way; for details see Schoute (18, p. 247-282).

This no doubt is the real cause of the scarcity of true whorls. But at the same time these considerations give us a hint as to where to look for true whorls. In the first place they are to be expected as rare exceptions in plants with wholly irregular phyllotaxis.

From the numerous instances which no doubt might be quoted, I shall give only a single one, which I happened to observe myself, in the spadices of an *Anthurium hybrid*, an *A. Andreanum* × *Scherzerianum*. In *Anthurium* the large amplecting spathe is followed by a great number of flowers, borne in the axils of aborted bracts. These flowers usually are arranged in various high patterns.

In this hybrid I determined the parastichies at the base, in the middle and near the tip of 100 spadices. In 41 of them the pattern from beginning to end was one of the main series, usually with 8 and 13 as the most conspicuous parastichies; 21 other spadices began with such a system, but higher up showed other patterns of the most varying kind, 8+12 (7 times) and 8+14 (n=4) being the most frequent, 7+8, 7+12, 7+13, 8+8, 8+10, 8+11, 10+13 and 12+16 being each represented once.

The remaining 38 spadices began at their bases with similar systems: 7+11 (n=10), 6+10 (n=6), 6+9 (n=5), 8+11 and 8+12 each twice, 7+14, 9+13, 9+14, 11+11, 11+15, 11+16 and 11+17 once each, and wholly irregular (n=6). Amongst these spadices a much lower percentage (only 12) kept the same system throughout (7 with 7+11, 3 with 6+10, one with 6+9, one with 9+14), evidently because of the smaller stability of these abnormal systems as compared to those of the main series.

Amongst these many and varied patterns only two whorled systems were observed, both already mentioned; one 8+8 at the tip of a spadix, the base and middle part being 8+13; the other was 11+11 at the base of a spadix, turning into 10+17 in the middle and into 10+16 at the apical region. We may be sure that these two patterns really represented true whorls. But at the same time it will be clear that their occurrence is wholly incidental and has no biological importance whatever. For us the only interest is that they undeniably are true whorls.

In these spadices connate flowers were to be observed in a few cases; the whorled portion of the spadices being so utterly insignificant, it is no wonder that in these parts no two-topped organs were observed.

True whorls further might be expected to have a better chance as soon as phyllotactical systems are built up in another way, not by a gradual elaboration from a small beginning. Such cases may perhaps be realized in different ways; about one of them, the case of the regularly dichotomizing stem, sufficient data are available.

As I have expounded elsewhere (25, p. 35) dichotomous branching, in taking away part of the phyllotactical system and replacing it by a new part formed on a transverse basis, must have the tendency to transform the systems, at least when the parastichy numbers are not too low, into other systems in which the parastichy numbers are more or less equalized. This view, enounced on a theoretical basis, appeared to be borne out by the facts to a large extent (ibid. p. 36-39).

The whorls of *Lycopodium*, intermixed with special systems of the form $n+(n+1)$, therefore are true whorls, not brought about by secondary phenomena. In *Lycopodium* accordingly no biastrepsis has been observed (Penzig 15, III, p. 562). On the other hand I observed connations as two-topped leaves in *L. carinatum* and in *L. Hippuris*. This may be brought about by the origin of two leaf centres in an unusually close proximity in the irregular systems.

Our conclusion therefore is that true whorls, though of subordinate importance, are realized in nature. A biological use to the plant, such as false whorls and especially binding whorls evidently often have, is not to be assumed; the fact that they are intermixed with spirals on a large scale, already might preclude the possibility of their being taken up into a construction scheme of biological interest.

§ 3. Conclusions.

1. True whorls are phyllotactical patterns in which the leaves arise in two sets of contact parastichies, having the same coordination number.

False whorls are those where the leaves arise in two sets of contact parastichies with unequal coordination numbers and where moreover through secondary causes the leaf primordia afterwards are united laterally so as more or less accurately to form whorls.

2. Accordingly the features of false whorls are the following.

They are characteristic for one or more (or all) leaf categories of the plant. In these leaf categories they are dominant, usually varying only with whorls of other leaf number.

In plants with binding whorls in highly exceptional cases the binding may ensue in a winding spiral order. If in such cases a sufficient growth in length follows and if the binding is firm enough, biastrepsis is the consequence. Biastrepsis therefore is limited to plants with binding whorls.

By the adaptation of heteromerous binding whorls to alternation, two leaves in a whorl may be crowded together and may partly fuse. The so-formed two-topped leaves are similar in outward appearance to the two-topped leaves due to dichotomizing of the leaf apex, and to those arising in irregular phyllotaxis by the induction of two leaf centres in unusually close proximity.

In growth whorls biastrepsis is not to be expected, and two-topped leaves may only arise in the very rare cases where the underlying original phyllotaxis is an irregular one.

3. The features of true whorls are the following. When varying, the newly arising systems are hardly ever whorled. Biastrepsis never occurs, but two-topped leaves may arise through the irregularity of the phyllotaxis.

4. False whorls, especially binding whorls, are wide-spread in vascular plants.

New cases of growth whorls were not recorded, but the whorls of the *Articulatae, Cupressaceae, Gnetales, Hydrilleae, Casuarinaceae, Hippuris, Labiatae,* of *other decussate Dicotyledons,* of *cotyledons* and *prophylls of Dicotyledons* all were shown, with more or less cogency, to be binding whorls. Floral whorls probably always are false whorls too.

5. True whorls are rare in vascular plants, as they cannot be built up in the usual way from a small beginning. As instances are put forward the very rare whorled systems occurring between many other anomalous systems in the irregular phyllotaxis of the *Anthurium* spadix, and the frequent whorled systems ocurring together with spiral systems in the dichotomizing stem of *Lycopodium.*

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Botanical Laboratory of the
Government University.

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