ON WHORLED PHYLLOTAXIS.

II. LATE BINDING WHORLS OF PEPEROMIA

By

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§ 1. Introduction.

In the first paper of this series (11) I described a kind of false whorls, which arose by the formation of some long internodes in an axis with crowded leaves, whereas most of the internodes remained quite short. The so formed growth whorls were easily to be recognised as false whorls, because there were no secondary displacements of the members, no metatopies.

In that first paper I remarked however that there must be still other kinds of false whorls, and in the present paper I will treat one of these other forms, a form termed by me binding whorls. The characteristic of these whorls is that in the mass of crowded leaf primordia, which may be arranged according to any system of phyllotaxis, the separate primordia are attached to their lateral neighbours and more or less firmly united with them.

I will not enter into a discussion of the nature of this binding, whether it may be brought about by the vascular bundles or by other means, as this is a separate subject; in this paper I hope to give evidence of the existence of such binding whorls and to describe them morphologically.

When a primordium is fastened to its lateral neighbours, and these again to their neighbours, a less or more horizontal chain will be formed. In most cases this chain will close at the other side of the apex, and so a ring, the future whorl, is formed. If however the one end of the row overlaps the other, the row is likely to continue itself without end, winding up in a spiral, as every member only can find a mate in the direction of such a spiral, all lower ones being inserted already in the lower coil. If then in the subsequent growth of the axis this spiral does not give way to the elongating forces, a torsion (Zwangsdrehung) is initiated.

The binding of the members of a whorl may probably appear at any stage, even before the first sign of the primordium is visible to us, and the tightness of the binding may also vary. In any case, the binding whorls of different plants are not quite the same in every respect, and the differences are such as may be brought about by differences in the time and the nature of the binding. The earlier the binding sets in and the tighter it is, the more displacement of the leaves will ensue: the members of one whorl by the subsequent growth will become equidistant and all situated at the same level; succeeding whorls will adjust themselves as much as possible to the available space and become either alternating, or in some cases superposed.

From all this follows that, when binding whorls exist, those cases must be clearest, in which the binding occurs very late in the development or is rather lax. The genus *Peperomia* will afford us examples of this case. In different *Peperomiae* spp. we have whorls, which as we shall see hardly show any metatopy at all, and some of them still exhibit with extreme clearness the original Fibonacci spiral, out of which the whorls are formed. The study of *Peperomia* will therefore form an excellent introduction to the study of binding whorls in other plants.

Before proceeding to the description of my present observations on *Peperomia*, I will mention what we find in the literature on the subject. In their splendid paper „Essai sur la disposition des feuilles curvisériées" (1, p. 80) the Bravais brothers briefly treat some cases of scattered leaves with the appearance of whorls.

Amongst their examples we find also two Peperomia spp. viz *Piper blandum* (= *Peperomia blanda* H.B. et K.) and *Piper inaequalifolium* (= *Peperomia inaequalifolia* Ruiz et Pavon). In both species, which have mostly ternary (*blandum*) and quinary or even octonary (*inaequalifolium*) whorls, they clearly recognise a normal Fibonacci spiral from the differences in distance between the leaves in every whorl, from the differences in the height of insertion and from the differences in the size of the lowest leaves of a shoot. As in paragraph 3 the same phenomena will be described

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3) I much regret not to have noticed this passage earlier, as I should have quoted in my former paper that they describe there too some elongation whorls, viz of *Lilium Martagon* and *L. superbum*. Their conclusion is quite the same as the one I got at, through they did not follow the genetic spiral from the zone of the scattered leaves through the whorls till unto the bracts. According to their observations in *L. Martagon* there may be 3 or 4 false whorls of 5 to 7 leaves each, rarely of 4 to 6 leaves; in *L. superbum* there were 6—8 false whorls of 8 to 10 leaves each; the divergence in the genetic spiral was 137° 30′.

in much more detail and the results of the Bravais will be fully confirmed, I will not dwell upon their observations here, but will refer to them later on, in my own descriptions.

To my knowing it is only 75 years afterwards that a study of the whorls of the *Peperomiae* again was undertaken. In a paper on false whorls (9) Goebel treats the same plants, without knowing of the description of the Bravais. The results of his observations are quite different from theirs, as he is inclined to consider the peculiar whorls of *Peperomia* as derived by contraction from a decussate phyllotaxis. To derive trimerous whorls from decussation, Goebel is obliged to suppose that two leaves of one pair and one leaf of the next pair remain together and so on. As evidence for his opinion he points to the fact that very poor shoots of *P. verticillata* may form dimerous whorls instead of tetra- or pentamerous ones, and to the other fact that transverse sections of buds show an arrangement of young leaves which is very much like an ordinary spiral arrangement. In this spiral he sees „pairs" of leaves, which do not arise simultaneously, and so he thinks to have shown, „ontogenetically and experimentally" that the whorls are derived from opposite leaves.

I hope to show in the following pages that the views of the Bravais were right and those of Goebel wrong; before coming to my own observations I want however to say some words about the kind of evidence needed for the derivation of one phyllotaxis from another.

As every phyllotaxis is built up anew in each individual shoot, a derivation in a phylogenetical sense has hardly any value; if we derive whorls from spirals or from pairs of leaves, we have to make clear, that by metatopy leaves assume a whorled position, after being formed in another phyllotaxis. To give decisive evidence for such a phenomenon no doubt experimenting would be the best plan;

but as the origin of a phyllotaxis is quite hidden to the eye, the only way of experimenting, is to cultivate the plant under abnormal conditions. In some cases such experiments have been taken rather succesfully (6, 7); in most cases however they are quite useless, as Nature herself takes infinite series of experiments in a matchless superior way, and these experiments lie open to those who take the trouble to look for them.

In studying false whorls the ideal case is that we have a sufficient number of axes, which have originally a well characterised spiral phyllotaxis, and afterwards form whorls in their middle part only. Observing the undisturbed original phyllotaxis in the base and top of every axis we may get full information about the original phyllotaxis and also whether it has been the same in the whole shoot; and in the meantime we may study the changed condition in the whorled zone, and perhaps its transitions from and to the undisturbed arrangement at the bottom and at the top. We had something like this in the stem of *Lilium Martagon* (11, p. 191) and we shall see in the present paper that some *Peperomiae* exhibit nearly the same ideal state.

The material I studied consisted of the collection of living *Peperomiae* of the Groningen botanical Garden. I will first give in paragraph 2 a short account of those, in which no whorls were present, while the third paragraph will contain a description of the different species of our Garden with binding whorls. The fourth and fifth paragraphs will finally be devoted to a discussion and to a summary.

§ 2. Species of Peperomia without any whorls.

Of these species our Garden contained the following: *P. prostrata* Hort, *P. scandens* Ruiz et Pavon, *P. eburnea* Lindl. and *P. metallica* Lindl. et Rod.

In all these four species, the vegetative leaves were arranged according to a phyllotaxis of the normal Fibonacci series. *P. prostrata* and *P. scandens* were always distichous, *P. eburnea* and *P. metallica* had scattered leaves.

The only one in which some tendency to whorl formation was present was *P. metallica*, as every now and then two leaves remained near to each other, without any regular distribution of the phenomenon.

With the exception of *P. eburnea* all four species flowered in our hothouse, and as the *Peperomiae* have terminal inflorescences it was worth while, in view of what we shall find in the following paragraphs, to pay attention to the phyllotaxis of the inflorescences.

In *P. prostrata* and in *P. metallica*, the inflorescences generally have normal phyllotaxis. In *P. metallica* where the vegetative leaves show the same disposition, the direction of the basal spiral of the inflorescence is, as might be expected, the same as that of the leaves.

Among seven shoots I examined in this respect, six showed in their leaves and bracts one and the same spiral; in the seventh the inflorescence was quite irregular, showing no basal spiral at all. In *P. scandens* finally the inflorescences were as a rule anomalous, showing such dispositions as 8 + 9, 9 + 9, 8 + 11 etc. The only conclusion we can draw from these facts is, that the phyllotaxis of the terminal inflorescence may be the direct continuation of that of the shoot.

§ 3. Species of Peperomia with binding whorls.

In this paragraph I have to treat four species, viz *P. blanda* H.B. et K., *P. Langsdorfii* Miq., *P. pulchella* A. Dietr and *P. rubella* Hook; I shall treat them separately.

a. *Peperomia blanda.* The leaves in this *Peperomia* are placed in whorls, mostly in dimerous and trimerous ones, but whorls of 4 and 5 leaves may occur also, and sometimes a single leaf is to be observed. Successive whorls have a certain tendency to be isomerous, but changes in the number occur rather frequently. One stout shoot e.g. had successively as whòrls 3, 4, 3, 2, 2, 2, 2, 2, 2, 2, 3, 2, 2, 3, 2, 2, 2, 2, 3, 3, 5 leaves.

The Bravais observed already that the ternary whorls have no equidistant leaves. They write (1, p. 80): „entre les trois feuilles de l'anneau, il existe deux grands angles et un petit; chaque grand angle est sans doute égal à 137° 30′, et le petit, à la divergence secondaire de la feuille 2, ou à 85°. Observez en effet la succession de ces petits angles; ils contournent la tige suivant une spirale continue, et en sept pas vous revenez au dessus du point de départ. Vous avez donc parcouru la spire secondaire par 3, dont la divergence est de 52° 31′, et vous êtes arrivé au dessus de la feuille 0 à la feuille 21 = 7 fois 3."

Their conclusion is therefore that the whole phyllotaxis is a spiral one with a normal divergence and that by the union of three leaves every time the whorls are formed.

We shall see that this conclusion is quite right and that it may be borne out by several other facts not observed by them. In the first place by the regular transmission of the different distances of the leaves. They only described the transmission after a ternary parastichy in ternary whorls. If we have however a shoot with two kinds of whorls, the rule of the transmission is somewhat more complicated. Fig. 1 gives the phyllotaxis of a shoot with four trimerous and eight dimerous whorls. In the trimerous whorls we see as they observed two members nearer to each other than to the third, and this phenomenon is transmitted to the higher similar whorls in a direction according to a rather steep right-hand parastichy.

This figure has been drawn, as the following figures in this paper, by Mr. R. Hoeksema, designer to the Groningen botanical Laboratory.

In the dimerous whorls the two members are not opposed,

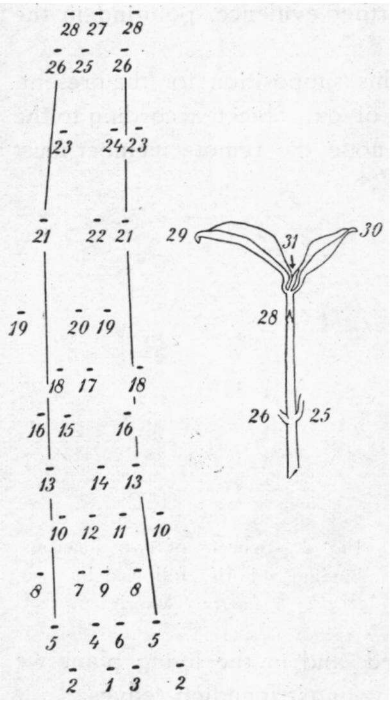


Fig. 1. *Peperomia blanda*, surface of shoot Nr. 4, $1/2$ natural size, and top of same, slightly magnified.

but at one side of the stem they are closer to each other than at the other side; this relation is transmitted according to a left-hand parastichy. The same phenomenon always returns in this species whenever dimerous and trimerous whorls are formed in the same shoot; the direction of transmission of the approachments is inverse in both.

This phenomenon becomes very natural, when we may assume with the Bravais that these whorls are formed out of an originally normal phyllotaxis. Fig. 2 represents a normal phyllotaxis with right-hand basal spiral. If 1 and 2 form a whorl, just as 3 and 4, the members of each whorl approach each other, and the pairs are placed over each other in such a way, that the approachment is transmitted according to a binary parastichy i.e. antidromously to the basal spiral. If however 5, 6 and 7 form a trimerous whorl, just as 8, 9 and 10, there must be pairs of approached members, ascending as the Bravais saw already, according to a ternary parastichy i.e. homodromously to the basal spiral.

We have therefore every reason to suppose that the regularity here mentioned, really depends upon the development of whorls out of a normal phyllotaxis; there is however as we shall see further evidence, pointing in the same direction.

Assuming the thruth of this supposition for the present, we may number the leaves of our object according to the genetic spiral. For the first node the remote member must be 2 (cf fig. 2), and the two approached members must be 1 and 3; whether 1 is the left or the right one is to be established from the direction of the transmission of the approached members.

As this is right-handed, the genetic spiral itself in consequence must be right-handed too, and therefore 1 is the left one of the pair.

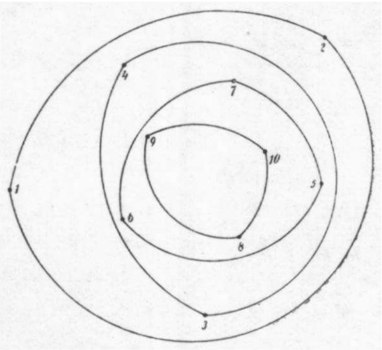


Fig. 2. Scheme of two dimerous binding whorls, followed by two trimerous whorls.

The following whorls may then easily be numbered, and in the living plant we thus may number even the young expanding leaves.

Now Goebel remarked already, that the young leaves in the bud do not exhibit whorls, but are more or less spirally arranged.

I have made no sections of the buds, but even without any sectioning it was clearly visible in our plant that the young leaves expanded in the sequence of a normal phyllotaxis. In fig. 1 to the right the top of the object is drawn, after removing the lower leaves. On 27 and 28 which were still represented in the diagram, there followed another pair of 29 and 30, 29 being clearly larger and further developed as 30; of the next pair only 31 was to be seen, 32 being still quite small and hidden between the other leaves. In many cases even the highest expanded whorl, of which the leaves are often not yet quite full grown will show differences in length according to the basal spiral.

These differences in size of the youngest leaves give us a first testing proof of the conception of the nature of the whorls: if this conception holds true, the numbering of the leaves, continued into the apical bud, must give a sequence coinciding with that of the size of the leaves.

In all six cases in which I could both observe the whorls and the expanding leaves this came true: not only the direction of the basal spiral was the same when stated in the two ways, but also the lower basal spiral always abutted on the higher one in the right way.

The two phenomena: the regularly distributed approachments of some of the leaves in their whorls and the differences in size of the expanding leaves are therefore the consequences of one and the same cause: the formation of the primordia in a normal spiral.

If this view is correct, we may ask how many leaves will most likely form a whorl. In our object there was a marked predilection for trimèrous whorls as appears from the following figures.

Number of whorls observed in:		
P. blanda	"main" axes	lateral shoots
Single leaves.......	—	3
2-merous whorls....	35	8
3- „ „	61	12
4- „ „	2	—
5- „ „	1	4

The „main" axes were those arising from the soil. Next to the trimerous whorls come the dimerous; of the other whorls it is very remarkable that the pentamerous whorls are still more numerous than the tetramerous ones; indeed the small number of tetramerous whorls is very striking. The explanation of this fact is probably the following.

For the formation of a dimerous whorl binding is necessary between leaf n and n + 1 on two sides. The two connecting lines are pieces of two different parastichies, one of the basal spiral short way, one of the basal spiral long way. In the same way we may find from what parastichies the three connecting lines in trimerous whorls are formed a. s. o. and then we get the following table.

Binding whorls.

Number of leaves in whorl	Connecting lines formed from parastichies:				
	basal spiral long way	basal spiral short way	binary	ternary	quinary
2	1	1	—	—	—
3	—	2	1	—	—
4	—	1	2	1	—
5	—	—	3	2	—
6	—	—	2	3	1

The 4- and the 6- merous whorls are therefore composed of pieces of three kinds of parastichies, the 2-, 3- and 5-merous of only two.

It is not impossible that the spatial relations between the primordia quite favour binding along two antidromous sets of parastichies, but are not favourable for the binding along three different kinds, of which two must be homodromous.

One question now still remains to be examined, viz if really the so formed whorls still show a phyllotaxis 5/21 (137° 8′ divergence) as the Bravais describe, or with the ideal angle of 137° 30′ which they suppose to be the case as well, or whether there is some metatopy. In order to settle this point we have first to determine the divergences of the leaves in every single whorl and further we have to determine the relation between the successive whorls and the way in which they are put together.

Now it is always difficult to estimate a divergence directly, but as far as I could see, there is really no indication of any horizontal displacements, at least not in the dimerous and the trimerous whorls.

I have tried to determine the distances of the leaves of one whorl directly in mM by measuring along the surface of the shoot, and thus to compare the ratio of their distances with the theoretical one of the normal phyllotaxis.

Of trimerous whorls I measured the distances in seven successive nodes of one and the same shoot. The distance of the 1st and the 2nd leaf of every whorl, expressed in the circumference was between ·32 and ·46 (mean ·39) of the 2nd and the 3rd leaf it was between ·33 and ·43 (mean ·38) and of the 3rd leaf and the 1st it was between ·17 and ·29 (mean ·23). If the divergence was the ideal angle these figures should have been ·38, ·38 and ·24, the approach of the observations to the theoretical value is remarkably close.

Of dimerous whorls I measured only four, and got for the distance between the 1st and the 2nd leaf ·32 circumference, of the 2nd and the 1st (long way) ·68, theoretically it should have been ·38 and ·62 which is quite a sufficiant approximation for so small a number of observations necessarily made in the rough.

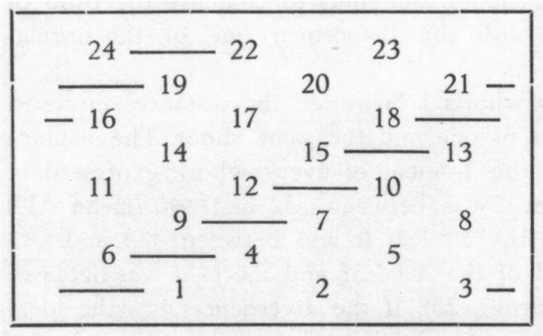
The absence of clearly discernible metatopy in the whorls makes it improbable that the whorls themselves should be displaced, so as to obtain a regular alternation.

In the dimerous whorls it was clear that such an alternation did not exist.

Whorl number 3 did not stand straight over pair 1, and its leaves were approached on the other side as those of pair 1. Pair 5 was approached on the same side as 1, but it lay a good deal more towards the anodic side. For a succesful statement the available series of dimerous whorls were not long enough: we shall have however good instances for this in *P. Langsdorfii.*

In the trimerous whorls we had to find in case of alternation on the same orthostichy as leaf nr 1 the leaves 9, 14, 19, as a glance at our scheme will show immediately. In the scheme the paired elements are connected by a hyphen. Over 1 it is only number 19 wich is the first that lies exactly in the same position, as the lowest leaf of a whorl; in our plant I therefore compared the position of 1 with 19, 2 with 20 etc. In one shoot with nine successive trimerous whorls these organs were nearly on the same orthostichy, or the higher one was placed somewhat to the anodic side of the orthostichy.

Scheme of alternating trimerous binding whorls.



So the trimerous whorls are unlike the dimerous ones as much alternating as may be consistent with the irregular distribution of the leaves in the whorls themselves, and unless the divergence has been altered by torsion, it must have been originally about 140° or somewhat more. For 18 divergences are seven circumferences or somewhat more; seven circumferences or 2520° divided by 18 makes 140°.

This divergence of about 140° agrees very well with what has been said about the dimerous whorls; if the divergence is 140° the fifth pair of leaves must stand 40°

on the anodic side over the first one, while with 135° it should lie just over the first pair.

Having in this way described the vegetative whorls of this plant as completely as I could, I now come to the beginning and the end of the shoot, which show both different conditions, and I will begin with the base.

The shoots of *Peperomia* may be divided for our purpose into two groups, the shoots arising from the soil as branches of subterranean rhizomes, and the lateral shoots developed above the surface; I have distinguished them above as main shoots and lateral shoots. In the main shoots the leaves of the subterranean parts are very small and hardly developed; for our purpose they are not very suitable objects.

As soon as a shoot reaches the surface, the development of the much larger normal vegetative leaves sets in. The whorl formation is present in the aborted subterranean leaves just as in the normal leaves; yet the transition of the small into the large leaves may betray the original spiral. The Bravais write about these leaves of our species: "petites et arrondies dans le principe, elles deviennent de plus en plus grandes, oblongues et acuminées, à mesure qu'on s'élève dans la spire génératrice. Il est aussi facile de reconnaître la suite des insertions de cette spire en se laissant guider par la forme et les dimensions des feuilles que par les propriétés connues de cette spirale."

Though my material of *P. blanda* did not allow me to confirm this observation of the Bravais, I saw quite the same phenomenon in *P. pulchella*, and no doubt the observation of the Bravais is quite right.

Lateral shoots were very abundant in my material, and of these I can give the following details. Every lateral shoot of *P. blanda* shows near its insertion on the main axis either at the left or at the right side a very small triangular red-coloured scale, a prophyll. On 34 lateral shoots 33 showed one prophyll, only one was instructed with two similar formations, one at each side. In those eleven cases, in which the lateral shoot was sufficiently developed to determine its basal spiral from its leaves, I found that without exception a prophyll on the left side was followed by a right-handed basal spiral, and inversely.

This relation is by no means a strange one: if the basal spiral, beginning at the prophyll, always runs first at the back side of the shoot, i.e. opisthodromously, the spiral must be as indicated.

Now in all cases examined, the spiral on being traced downward, abutted quite naturally in the prophyll as its first number. The basal zone of every shoot appears therefore to have the beginning of the same phyllotaxis but is subject to other organ-building laws. However short this zone may be, it forms one, or rarely two, leaves of a wholly different nature, and the whorl forming does not range there. The correspondance described above between the position of the prophyll and the direction of the basal spiral of the leaves is therefore a new proof of the correctness of the view of the Bravais.

I must now treat the end of the shoot. In those shoots that come to the formation of an inflorescence we get hold of new means of putting the same conception to a proof. In the first place the transition of the vegetative leaves into bracts, though rather abrupt, is not absolutely sharp.

The leaves of the last vegetative whorl, when quite full grown, show differences in size according to the original basal spiral.

These differences make the last whorl rather like one of the apex of a non-flowering shoot, but it is unnecessary to say that the phenomenon is quite another one. In the non-flowering shoot the differences proceed from differences in age and they will disappear as soon as the leaves are full-grown; in the second case the differences are the expression of the diminishing period of the formation of vegetative leaves.

The inflorescence itself affords another testing proof of our views. The bracts in *P. blanda* — and consequently also the flowers — are arranged with few exeptions according to a normal spiral. On 18 inflorescences 16 showed a normal spiral, one a 1 + 4 system and one 4 + 4. Of the 16 regular cases there were 15 in which the direction of the basal spiral could be compared with that of the lower phyllomes, either by the position of the prophyll or by the properties of the whorls. In all these 15 cases the direction of the spiral was the same in the leaves and in the bracts, as might be anticipated,

We therefore conclude that when in the region of the bracts the whorl-forming causes disappear, the same original phyllotaxis appears again, undisturbed and unchanged. If it were not for the shortness of the basal zone, the "ideal case" would be fully represented.

Before proceeding to the next species I have to remark that there was a certain tendency in the lateral shoots to be homodromous with their main axis. On 34 lateral branches I observed, 24 were homodromous, 10 antidromous to their parent-axis. At first sight this fact does not seem to pertain to our topic; but we must consider that if the whorls were true whorls, it was inexplicable how the direction of the spiral in the inflorescences of the lateral branches could depend on the direction of the spiral in the inflorescence of the main axis, as the lateral branches spring from the axils of members of the whorls. From our point of view it is quite natural that the main axis which is properly spiral throughout, should bear lateral spiral shoots with antidromous phyllotaxis.

b. *Peperomia Langsdorfii* is one of the socalled decussate species; the leaves are nearly always placed in dimerous whorls. Only under the terminal inflorescences may we find a tetramerous or a trimerous whorl, and occasionally we may find a weak shoot with some single leaves. So I observed one shoot with 1, 2, 1, 1, 1, 1, 2, 2, 2, leaves at the successive nodes, the single leaves being placed in a regular normal spiral.

On closer examination the dimerous whorls have approached pairs of leaves in the same way as in *P. blanda*; the transmission of the approachment is regular according to a definite parastichy.

So the supposition readily presents itself that in this species too the dimerous whorls are formed out of a normal basal spiral, which must be, after what we have seen, antidromous to the direction of transmission.

The prevalence of dimerous whorls quite fits in with what had been said of *P. blanda* about the larger probability of 2-, 3- and 5- merous whorls.

This supposition could be checked in several ways. In the first place we had the shoot already mentioned with four successive single leaves. These leaves were placed in a normal spiral with a divergence of about 135° or more, and the following three dimerous whorls showed a transmission of the approachments in an antidromous direction; the leaves in these dimerous whorls stood in the places, where they might be expected to stand from the assumption of one continuous basal spiral.

In the second place the distances of the leaves in the dimerous whorls were as far as could be measured, quite undisturbed distances of two successive leaves in a normal spiral. In one shoot I measured the horizontal distances along the surface in five whorls; the mean relation between the two distances in a whorl was as 39 to 61 (largest deviations 34 : 66 and 42 : 58) which would imply a divergence of 140°.

Further evidence was given by the following facts. In the shoots of *P. Langsdorfii*, just as in those of *P. blanda*, a difference in size was to be seen in the expanding leaves according to the same spiral as stated from the transmission of the approachments; at the beginning of every shoot I found again a single lateral small red-coloured prophyll; those shoots with a left prophyll here too had a right-handed spiral and inversely; the last vegetative leaves under the inflorescence, even when quite full grown, showed diminishing sizes according to the original spiral.

In one shoot with eleven dimerous whorls and one trimerous one under the inflorescence, I took the following measurements in the trimerous whorl:

leaf	23	petiole	5	mM.	blade	23	mM.
„	24	„	5	„	„	19	„
„	25	„	4	„	„	13	„

In those cases where the inflorescence showed a normal phyllotaxis of the bracts (seven cases against two with irregular systems in my observations) the direction of the basal spiral in the inflorescence agreed again with that stated before by the other means. We may therefore safely infer that *P. Langsdorfii* forms quite analogous whorls as *P. blanda*, only with a marked prevalence of the dimerous binding.

As the material was very convenient for the study of the alternation of the dimerous whorls, I made some observations thereon. In a certain shoot with 12 dimerous whorls I observed the following conditions.

Just as in the shoots of *P. blanda* with dimerous whorls, pair 5 was approached at the same side as 1, but it was placed a good deal more to the anodic side. The first pair that was placed rather exactly over pair 1 was pair 10.

From this we may calculate the original divergence with much more accuracy than from the direct observation. The first leaf of pair 10 is leaf 19, between 1 and 19 there must be 18 divergences; and as there are seven coils of the spiral between 1 and 19, the divergence, unless altered by torsion, must have been 7 × 360° : 18 = 140°. It is rather curious that we found the same divergence in the trimerous whorls of *P. blanda.*

The lateral shoots showed again a tendency to be homodromous tho their parent axis (seven homodromous against two antidromous shoots observed).

c. *P. pulchella.* This species, often called *P. verticillata,* shows a preponderance of pentamerous whorls. From the foregoing we might have expected that the whorls with other numbers of leaves might have been chiefly those with 3 and perhaps with 8 leaves: in *P. inaequalifolia* the Bravais found pentamerous whorls and occasionally one with eight leaves.

In our species the conditions however were different. What I observed is given in the following table.

P. pulchella. Number of whorls observed

with number of leaves	main axes	lateral branches.
1	—	1
2	—	5
3	36	3
4	179	51
5	395	65
6	47	1

Instead of a curve with two maxima on 3 and 5, we see a curve with a single top on 5 and a rather large amount of cases of tetramerous whorls. This forms a striking contrast with *P. blanda* where tetramerous whorls were rare.

For the preponderance of whorls with number of the Fibonacci series I gave above the explanation, that only those whorls can be formed out of pieces of two sets of parastichies; if there are only two sets of contact parastichies, as is the common case, those whorls will have a much greater chance. Whorls of four and of six leaves can as we have seen on p. 138 only be formed out of pieces of three sets of parastichies, and we have to consider this case here somewhat more in detail.

We might at first suppose that in those cases where at the moment of whorl formation three sets of contact parastichies exist, the binding of the primordia might occur at random along the different parastichies. The result should be that the whorls in such shoots were heteromerous; in the case of basal spiral, binary and ternary contact parastichies as connecting lines, we should have the formation of trimerous, tetramerous and pentamerous whorls, in an irregular succession. In the case of binary, ternary and quinary contact parastichies, we should expect four kinds, from pentamerous up to octomerous whorls, in the same irregular succession. This was however not what our plants showed: the tetramerous and the hexamerous whorls were often as regularly transmitted as the pentamerous ones. It was not difficult to find shoots with 9 or 10 successive tetramerous whorls, though in other shoots there was an oscillating between two or three kinds of whorls. To give an idea of the degree of constancy I give below the number of leaves of 16 of the shoots I invested. Among those are the most regular and the most irregular shoots I observed and some intermediate ones; I arranged them according to a diminishing regularity.

Shoot nr.	Number of whorls of different number of leaves in sixteen shoots of *Peperomia pulchella*.
24	9 × 4 (i. e. nine whorls of four leaves each)
33	21 × 5
16	11 × 6
30	10 × 4, 8 × 5

Shoot nr.	Number of whorls of different number of leaves in sixteen shoots of *Peperomia pulchella*.
36	3 × 3, 9 × 4
52	3 × 6, 5 × 5
54	8 × 4, 3, 8 × 4
34	15 × 5, 4, 3 × 5
4	20 × 5, 4, 2 × 5, 4, 5
70	4 × 4, 10 × 5, 4, 5, 8 × 4, 5, 3 × 4
13	5, 2 × 4, 5, 4, 2 × 5, 4, 6 × 5
35	3 × 5, 4 × 6, 5 × 4
59	3 × 4, 2 × 5, 4, 2 × 3
58	5, 6, 3 × 5, 4 × 4
26	4 × 4, 5, 4, 2 × 5, 3, 5, 4, 5, 4
10	6, 2 × 4, 2 × 5, 4, 5, 4, 3 × 5, 4, 20 × 5.

The first three shoots were wholly homomerous, 30, 36 and 52 showed only one transition, the next two had two transitions, but returned to their first kind of whorls, then we have three, nr. 4, 70 and 13, which oscillate several times between two kinds of whorls, while the last five have three kinds of whorls, with an increasing amount of transitions.

Even in those most irregular shoots we can easily see, that the whorls do not succeed each other by mere chance, but that there is always a certain tendency in the next whorl to have the same number of leaves as its predecessor. Perhaps the best way of demonstrating the tendency to homomery is the following one. The mean length of the homomerous parts of the main shoots I observed was

for the 3- merous whorls 2·6 whorl.
„ „ 4- „ „ 2·6 „
„ „ 5- „ „ 5·2 „
„ „ 6- „ „ 4·7 „

Now we need not go far into the theory of probability to conceive that with only 47 hexamerous whorls amongst a total amount of 657 whorls, chance would not give us a mean length of 4·7 whorl for the hexamerous parts of the shoots, and that this is only brought about by a rather strong tendency to homomery.

To explain this tendency to homomery in four- and in six-leaved whorls, we may make the following supposition.

When in an apex with leaf primordia binding is possible according to three sets of parastiches, there will always be one of them, the middle one in secondary number, which will be situated much more favourably for the origin of bindings than the others; and of the two other sets of parastichies there will likely be one, which is more fitted for issuing bindings than the other one. If e. g. the three sets of parastichies are the genetic spiral, the binary and the ternary parastichies, the bindings will probably appear first in the binary parastichies, and in some cases the genetic spiral will come second, in other cases the ternary parastichies will be more appropriate than the genetic spiral. Now we can easily understand that in the first case tetramerous whorls will result, in the second case pentamerous.

In fig. 3, a theoretical phyllotaxis of the main series is reproduced. If the first leaf 1 is connected to 3 and 2 to 4, which connections are represented by heavy lines, 1 will in no other way be able to establish a connection at the other side as with leaf 4, while 2 may unite itself to 3 or to 5. Now our supposition was that the basal spiral was more likely to form bindings than the ternary parastichies,

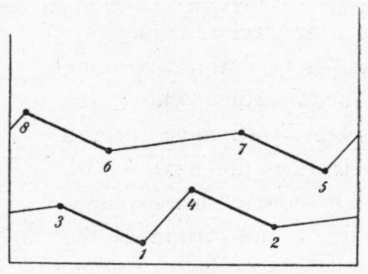


Fig. 3. Scheme of the formation of tetramerous binding whorls.

and so 2 will unite itself to 3, and a four-leaved whorl will be the result. Between the leaves 5—8 the same game will be repeated, and so a number of tetramerous whorls will ensue, unless the relation of bulk between apex and primordia changes and other sets of parastichies will be more fit for new connections.

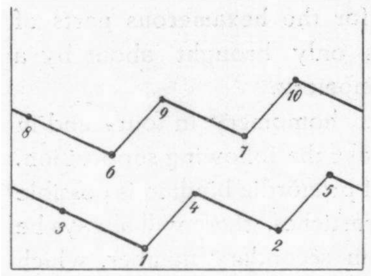


Fig. 4. Scheme of the formation of pentamerous binding whorls.

If however the ternary parastichies are more appropriate than the genetic spiral, we will have as in fig. 4 that, after the binding of 1 to 3 and 2 to 4, 1 unites to 4, and 2 only joins 3 via 5, so that a pentamerous whorl is formed; in the higher leaves pentamerous whorls will appear in the same way.

Hexamerous whorls will be formed according to this view, when the ternary parastichies are most appropriate for the appearing of bindings, the binary parastiches come next, and quinary will only be formed when no other parastichy for a connection is available. In fig. 5, 1 is united by heavy lines to 4, 2 to 5 and 3 to 6; after the formation of these unions 2 joins 4, 3 unites to 5. For 1 there is no other second connection besides 6, thus forming a hexamerous whorl; the leaves 7—12 must form in their turn the next whorl.

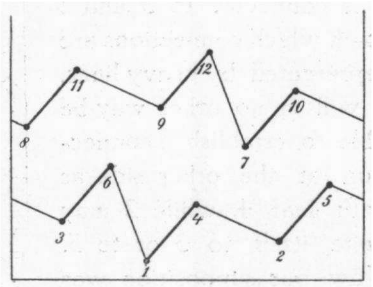


Fig. 5. Scheme of the formation of hexamerous binding whorls.

Of course this explanation of the origin of the binding is rather hypothetical, but it is in so far up to the purpose, as it gives us an idea how a regularity in whorl formation, so as we found it in *P. pulchella*, may originate.

I now come to the description of the particularities of the whorls themselves, and I shall treat separately first the pentamerous and then the tetramerous and the hexamerous whorls.

The Bravais brothers write that in their species with pentamerous whorls, viz *P. inaequalifolia*, the leaves were inserted at somewhat different heights, and that it was easy to recognise thereby a single basal spiral with a divergence of 137° 30′. In my material there were, as we shall see, also very slight differences in height, but in such a small degree that I only saw them when, after having found out the basal spiral by other means, I attentively sought for them. In horizontal sense the leaves were placed more or less regularly at equal distances, and the remaining differences were not transmitted to the higher whorls in a regular way.

One might be therefore inclined to think one moment that in this species we really had true whorls; but closer examination revealed with full certainty that these whorls were just the same as in the preceding species.

In the first place we had the differences in size of the expanding leaves; in all cases a very good quincuncial order of development was to be observed. In the second place, though the full-grown whorls themselves no longer betrayed their origin, the axillary shoots did. For it was very remarkable in the stout branched stems with pentamerous whorls, that the lateral branches were placed in the axils of part of the leaves in a regular way. In most cases two leaves of a pentamerous whorl were fertile, with one single sterile leaf between them; and the fertile leaves of the successive whorls were placed on two non adjoining but parallel quinary parastichies of the 5 + 5 system. This remarkable distribution was therefore transmitted in a peculiar way, quite analogous to the way of transmission of the horizontal distances in the dimerous and trimerous whorls.

Compared with the spiral found from the expanding leaves, the transmission was in antidromous direction. Now if we imagine pentamerous whorls formed out of a normal spiral the numbers of the first leaves in the whorls must be 1, 6, 11 etc; the first leaves must ascend in the direction of a quinary parastichy i. e. antidromously to the basal spiral.

As the buds developed in the axils of two leaves with one sterile leaf between them, it might be that the first two leaves of every whorl were fertile, or the second and the third etc. The spiral given by the expanding leaves soon showed, when traced downward, that it was the two first leaves, as might be anticipated as the most natural state of things. For these leaves on the moment of whorl formation are farthest in development and so probably their axillary buds are.

In the table below I give the length in mM. of the side branches of the main axis nr. 2, for those branches that were clearly visible and formed at least a 1 mM. bud.

Peperomia pulchella, size of lateral branches

Nr. of subtending leaf	Length of axillary branch	Nr. of subtending leaf	Length of axillary branch	Nr. of subtending leaf	Length of axillary branch
57	120	72	61	82	26
61	5	73	4	83	24
62	1	76	54	86	21
66	84	77	42	87	21
67	65	78	7	91	7
71	72	81	31	—	—

The numbering of the leaves is derived from the development of the buds, and checked by the size of the expanding leaves at the apex. In whorl 56—60 only the second leaf was fertile, in the whorls 71—75, 76—80 and 81—85 the third leaf also had a somewhat developed bud, but in no whorl were buds developed in the axils of the fourth and fifth leaves. Yet in every axil a very small bud, less than ·5 mM. was to be seen; obviously in one whorl the first leaves were so much advanced in their development at the moment of whorl formation, and their buds too, that for the buds of the following leaves there was no occasion left for development.

The differences between the first and second branches in every whorl agree also with this view; with the exception of the branch from 87 which equals that of 86 every second branch is smaller than the corresponding first branch.

Once being able to mark the original basal spiral in any whorl of this species, I wanted as remarked above to examine more accurately the position of the leaves in the whorls, whether the original differences in position had been completely swept away by metatopy or whether small remnants of them had still remained.

The latter proved to be the case. In every pentamerous whorl there were two of the leaves, which were placed somewhat higher than the other three; and these two were separated by one leaf. The difference was very small, and might easily escape the unsuspicious observer but especially in those cases where the leaves had dropped and the natural scars clearly indicated their places, it was very clear and unmistakable. The phenomenon was transmitted to the higher whorls in an antidromous direction, as should be the case.

In fig. 6 I have drawn the apex of shoot nr. 4, (see the table on p. 148); the distance of the leaves in the whorls is exaggerated and especially the differences in height of the insertion are drawn too large. I took this example, as we had here a succession of different whorls; 5, 5, 4, 5, 5, 4, 5. In the lowest whorl the two highest leaves are obviously 4 and 5, and as the two highest leaves in the next whorl are placed at the left side of them, the basal spiral must ascend antidromously, so that the left leaf must be 4, the right one 5.

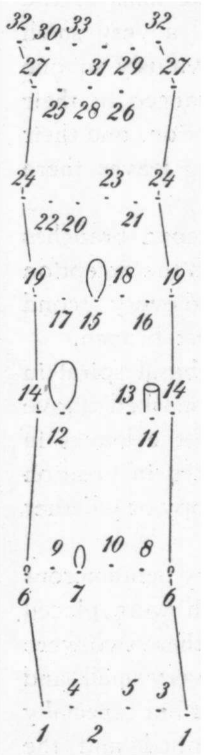


Fig. 6.
Peperomia pulchella.
Surface of the top end of shoot nr. 4

Continuing this numbering, we see that the highest leaves in the following whorls, notwithstanding the heteromery of the whorls, always bear the highest numbers; and further, as the buds are also indicated in the drawing, we see too that only the first leaves of some of the whorls are fertile. As soon as a tetramerous whorl follows on a pentamerous whorl, the regular transmission of the bud formation must be spoiled in the higher ones, therefore after buds in the axils of 6 and 7, and in those of 11 and 12, we do not find buds in the axils of 16 and 17 but of the lower leaf 15, which, if it had remained in the third whorl, would have been the highest and a sterile one.

I have quoted already the statement of the Bravais that the divergence of the leaves in their *Piper inaequalifolium* was 137° 30′. I am much inclined to suppose that their predilection for the ideal angle was the chief source of this statement. For in my *P. pulchella* the leaves in the whorls were sufficiently equidistant to be sure that in the pentamerous whorls the divergence was about 144° (and in the hexamerous about 120°). Without any doubt we have here evident metatopy.

The fact that the dimerous and trimerous whorls of the foregoing species did not show any horizontal metatopy, while these pentamerous whorls do, must be explained probably by the fact that in dimerous and trimerous whorls there is room enough for the developing leaves, whereas in the more crowded pentamerous (and hexamerous) whorls the available room must be divided and as the leaves are all of about equal size, tends to be divided equally so as to make the leaf insertions equidistant.

I have more over tried to establish the relation in position between successive pentamerous whorls. In the same way as it has been determined for trimerous whorls, we may find for pentamerous ones that in the same orthostichy with leaf number 1 we ought to find in perfectly regularly alternating binding whorls the leaves 14, 22, 35, 43, 51 etc. In our fourth shoot, which had no less than 20 successive pentamerous whorls, I found that these leaves did not lie on an orthostichy but on a very steep parastichy, homodromous to the basal spiral. Instead of leaf 43 it was rather accurately 42 which lay just over 1. The divergence, unless altered by torsion, must have been originally therefore about 140° 30′, as the basal spiral makes 16 coils between 1 and 42; and 5760°: 41 makes 140° 30′. The agreement with the divergence found in the dimerous and trimerous whorls is astonishing close. If therefores in every whorl the divergence may be taken for 144°, the divergence between the "cyclur" and the "cyclarch" of Schimper and Braun must have been in this shoot 126° 30′ whith a "negative prosenthesis" of 17° 30′, as $5 \times 140^\circ\,30' - 4 \times 144^\circ = 126^\circ\,30' = 144^\circ - 17^\circ\,30'$.

The tetramerous whorls showed, as might be expected, in many respects intermediate conditions between the trimerous and the pentamerous ones. In many shoots the four leaves of a whorl were equally distributed around the axis, so that the insertions were at about 90° distance of each other; differences in height of insertion were not to be found. In those cases the tetramerous whorls were no suitable material for investigation; at least the full grown well developed whorls without axillary branches were not.

Happily in other shoots the horizontal metatopy was not so complete, and in every whorl one of the four distances was evidently larger than the three other ones. The distribution of this large space was again quite regular: in the next whorl the large distance was at the opposite side of the axis, in the third whorl it was just over the large space of the first whorl: this was of course only possible by the fact that the tetramerous whorls themselves were superposed whorls.

In fig. 7 I give the five whorls of one and the same young shoot nr. 50; the nodes of it were cut, and drawn from above in the same position as they had occupied in the living shoot. In the first whorl two of the leaves are much smaller than the two others, and the large space is turned to the bottom side of the drawing. From this the numbering of the figure may be derived with sufficient certainty. On p. 138 we saw that in tetramerous whorls one of the four distances must be made out of a divergence of the genetic spiral; it is clear, that the large space must be this one, and as the two small leaves must be 1 and 2, the numbering cannot be given in another way as has been done in the figure.

When we continue the same numbering in the four higher whorls, all the large spaces precisely get those numbers at both side which only differ one unity, as might be expected, and in the highest whorl, which was still expanding, the leaves 19 and 20 are the smallest and youngest. I believe therefore that in this case as in the former ones the proof has been given, that these whorls are formed out of a normal spiral phyllotaxis. The superposition of the whorls would give us an original divergence of 135°, as the ninth leaf is over the first one in exactly the same position.

Whether this superposition kept true in longer series of tetramerous whorls I did not observe, perhaps the divergence was therefore slightly different from 135°. By metatopy this divergence of 135° was changed into a more or less regular succession of 90°, 180°, 90°, 180°

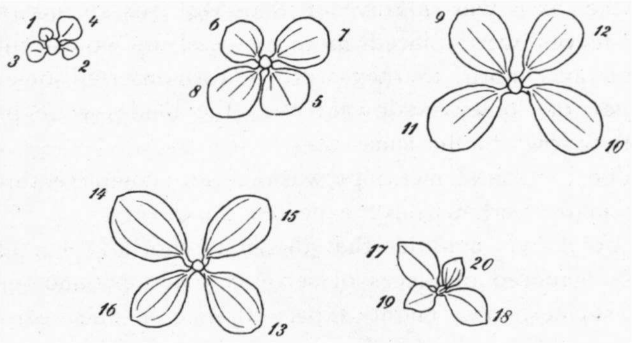


Fig. 7. *Peperomia pulchella*, five successive whorls of shoot nr. 50, slightly magnified.

etc.; in those cases where the "large spaces" were to be observed, this metatopy was incomplete.

The scheme of these whorls is

9	12	10	11
6	7	**5**	8
1	4	2	3

The lowest number of each whorl has been printed in bold-face type.

As mentioned above Goebel regarded these tetramerous whorls as formed by the contraction of two dimerous ones. From our observations it follows that in every whorl there are two opposite younger and two opposite older leaves; and the distinction of two dimerous whorls in every tetramerous whorl may therefore be kept up.

There is however no doubt that the real way of development of these tetramerous whorls does not go through a decussate state, and a phylogenetic derivation from dimerous whorls is neither to be supposed.

For the hexamerous whorls I studied in detail shoot nr. 7, with eight hexamerous whorls. In these whorls the leaves were, by their still more crowded position, rather exactly placed at equal distances, but, as the circumference of the axis was hardly large enough for six insertions, the leaves were placed more or less in two alternating trimerous whorls, as they were in turn inserted somewhat higher or somewhat lower; even the blades were placed in two rows in the same way.

The horizontal metatopy was therefore complete, through one might perhaps have expected the reverse.

For if we consider that the first whorl, 1, 4, 2, 5, 3, 6 is composed of pieces of secondary, ternary and quinary parastichies, one might expect that e. q. the horizontal distance of 6, 1 would be smaller than that between 4, 2. It appeared however that the horizontal distances only showed small differences without regular distribution and were all nearly about 60°.

The eighth whorl, which was composed of the expanding leaves, gave the original spiral with full certainty, and from this whorl it might be followed downward until the base of the shoot.

The mutual position of the hexamerous whorls was, as far as might be judged, exactly superposed in such a way that the trimerous whorls alternated regularly. There were therefore three orthostichies on which the lower leaves of every whorl were placed and three with the higher leaves of the whorls.

The only possible arrangement must therefore have been:

24	19	22	20	23	21	24
16	14	17	15	18	13	16
11	9	12	7	10	8	11
6	1	4	2	5	3	6

In this scheme the lowest member of every whorl has again been printed in bold-face type. The original divergence must have been in this case again, unless torsion had taken place 140°, out of which by metatopy a regular succession of 120°, 120°, 180°, 120°, 120°, 180°, etc. had grown.

In our shoot it was not only visible that over leaf 1 stood leaf 19, the first leaf of the fourth whorl, but also 37, the first leaf of the seventh whorl, so that the opposition of the hexamerous whorls must have been rather accurate.

In the cases described in the foregoing pages, the whorls were all very regular and undisturbed. In two shoots I observed however a strange deviation of the common condition. Fig. 8 represents five successive whorls, figured from above and from aside, of shoot nr. 41, which had the following whorls: 3 × 5, 4, 3 × 5. The first whorl had two leaves in an accurately superposed position, one very small leaf under one of normal size: this whorl looked as if a supernumerary leaf of a higher whorl sticked to a tetramerous whorl. From the size of the leaves only one spiral was to be chosen, starting from the small leaf under the normal one. If we continue this numbering upwards, we get without any uncertainty a normal pentamerous arrangement in the fifth whorl, which was to be continued in the sixth and the seventh; in this last and expanding whorl it coincided with the order of the leaves according to their size. The first four whorls in this way got the numbers, given in fig. 8. If we try to read this shoot in terms of normal whorls, which have been disturbed by the sticking of some of their members to a wrong whorl, we had to suppose that the

1st whorl received from higher whorl 6, gave to higher
whorl 5.

2nd whorl received from higher whorl 11, gave to higher
whorl 10.

3rd whorl received from higher whorl 16, gave to higher whorl 15.

We might however with as much reason suppose that the binding had not taken place here in the ordinary

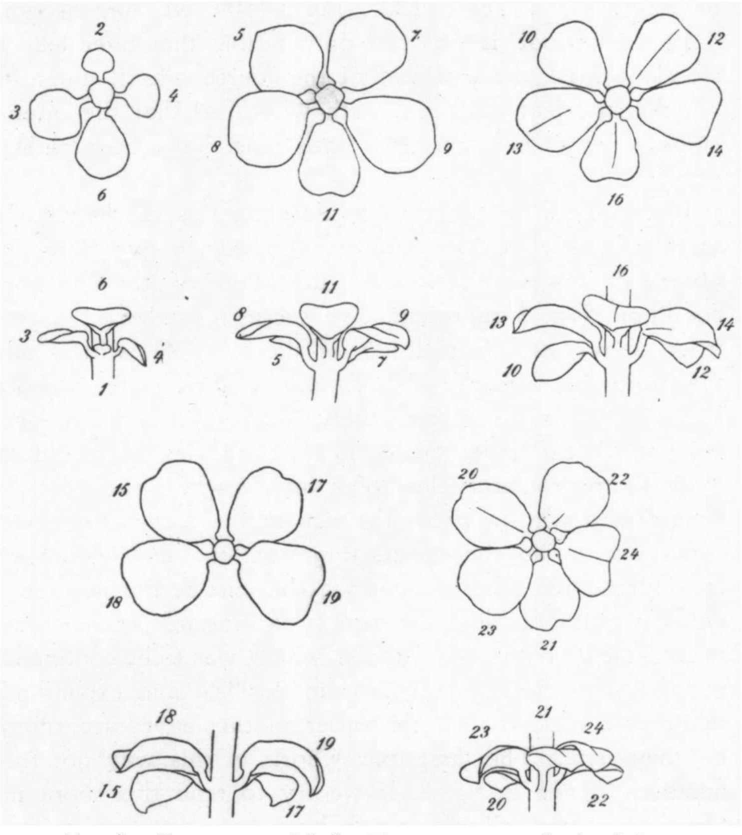


Fig. 8. *Peperomia pulchella*. Five successive whorls of shoot nr. 41, slightly magnified.

regular way, but that leaf 6 had been left alone, and that in the 2nd and 3rd whorl from leaf 5 and 10 binding had taken place after one single binary and one ternary parastichy, untill the whorls closed at the leaves 11 and 16.

In the fourth whorl the binding was quite analogous but the highest leaf 21 was not taken into the whorl, so that from the fifth whorl upward the normal conditions returned. Perhaps this last explanation is the simplest, as the former one leaves unexplained why the sticking of leaves to other whorls is transmitted rather regularly.

Our observations have made clear, that, if not quite in the same way as in *P. blanda* and *P. Langsdorfii*, the whorls in *P. pulchella* yet undoubtedly showed their origin out of a normal spiral; we may now ask whether the beginning and the end of the shoot may confirm our results in the same way as previously.

The base of every shoot here was not instructed with a single prophyll, but with two similar ones, placed laterally at both sides. Therefore it was impossible to compare their position with the direction of the spiral of the leaves, the only thing to be done was to examine which was the relation of the prophylls to the spiral.

Now the first normal leaf of every shoot was placed at the front side of the shoot, and somewhat to the left or to the right. In those cases where the spiral was right-handed, it was placed somewhat to the left, and inversily. This means that the spiral ran from the first (left) prophyl opisthodromously to the other one, and then to the first leaf: the opisthodromy of the spiral agrees with our observations in the preceding species.

The first vegetative leaf of every shoot, though mostly placed in a tetramerous whorl, was bigger than the other ones, and once aware of this difference, it was always easy to start the spiral from beneath.

In the position of the leaves on the lateral branches there was one remarkable peculiarity, viz that they nearly always started with a few tetramerous whorls, and then went to pentamerous ones. By this fact the frequence of the tetramerous whorls on the (often short) lateral branches was relatively much higher than on the main axes (see p. 146). To explain this we must assume that in the lateral branches after the prophylls have been formed, primordia are developed with prevalent binding in the binary parastichies, in the second place binding in the basal spiral and only where it could not be done otherwise in the ternary parastichies.

The transition to the pentamerous whorls will follow, as soon as by the relative growth in bulk of the apex the ternary parastichies become contact parastichies in the moment of binding, while the basal spiral loses its contact.

For sake of illustration I give the numbers of whorls of the lateral branches of shoot nr. 3.

Shoot from the axil of leaf nr.	Number of whorls.
71	2 × 4, 6 × 5.
75	2 × 4, 6 × 5.
76	2 × 4, 6 × 5.
80	2 × 4, 4 × 5.
81	2 × 4, 5, 2 × 4.
85	2 × 4, 2 × 5.
90	4, 2 × 5.
91	2 × 4, 2 × 5.

We should now still have to treat the end of the shoot, but as our species did not flower at the times of investigation, this is for the moment impossible.

On nine lateral branches, of which I determined the direction of the basal spiral, six were antidromous to their parent axis, three homodromous; a tendency to antidromy is therefore again to be observed as in the foregoing species.

d. *P. rubella*, a tiny form with red coloured stems and lower surfaces of leaves, always shows whorls of variable numbers, from trimerous to hexamerous, while occasionally dimerous whorls and single leaves may be observed. One of the shoots had the following whorls: 3 × 3, 4, 5, 4, 3 × 5, 6, 3 × 5, 4. By the smallness of the parts, it was somewhat less convenient for examination, and as it will only corroborate our results, but give no new facts, I shall treat it briefly.

In the trimerous whorls I found regularly two approached leaves, and the approachment was transmitted antidromously to the basal spiral; in the pentamerous whorls I found no regularly distributed irregularities. The axillary buds developed in the axils of the first numbers of a whorl, in the shoot mentioned above I observed the following relations.

5th	whorl,	5	leaves,	lateral	shoot	from	2nd leaf.
6th	„	4	„	„	shoots	„	1st, 2nd, 3rd leaf.
7th	„	5	„	„	shoot	„	2nd leaf.
8th	„	5	„	„	„	„	1st „
9th	„	5	„	„	„	„	1st, 2nd, 3rd „
10th	„	6	„	no lateral shoots.			
11th	„	5	„	„	„	„	
12th	„	5	„	lateral	shoot	from	1st leaf.
13th	„	5	„	„	„	„	1st and 2nd leaf.

The regularity is therefore not so great as in *P. pulchella*, but still very remarkable, and sufficient proof for the real existance of the assumed original spiral.

The expanding leaves at the apices of the non flowering shoots were again very strikingly different in size according to their succession in the spiral. Every lateral shoot began with one small lateral prophyll, and the spiral ran opisthodromously from this prophyll to the first leaf, which was accordingly placed at the other side somewhat backwards.

On 17 flowering shoots only two had an inflorescence with anomalous phyllotaxis; one with 3 + 4 and one quite irregular. Of the remaining 15 there were 14 of which the basal spiral ran in the same direction as the spiral as determined from the leaves or from the prophyll; only in one case the direction was inverse. In this shoot, a small lateral shoot, the prophyll was at the right side, the spiral, as determined from the leaves was left-handed (one trimerous and one tetramerous whorl), as it should be according to the position of the prophyll, but in the inflorescence the spiral was right-handed. This exception, the only one in all my observations does not in the least invalidate the results, as a change in direction of a basal spiral will occur in many plants as a rare phenomenon.

On 18 lateral shoots 14 were antidromous to their parent axis, 4 homodromous.

§ 4. Discussion.

From our observations it follows that the Bravais brothers were right in considering the whorls of *Peperomia* as formed out of a normal spiral phyllotaxis. This transformation is not a phylogenetic but a developmental one. The whorl formation sets in apparently only very late during the development of the leaves so that many traces of the original spiral disposition remain.

Even without these traces it would however be possible to give proof of the real existence of the spiral in the whorls by the fact that the beginning and the end of the shoot are not subject to the whorl formation and that it is only in the vegetative leaves that we do find the whorls. The prophyll and the bracts in the inflorescence are not placed in whorls, and now it would be unexplainable how the spiral of the bracts could be in accordance with the position of the prophyll, if we might not assume that one and the same spiral reigns throughout, but is only obscured like the moon during an eclipse. As soon as the whorl forming factors give way, the spiral reappears unchanged in every respect.

Now our certainty is still raised by the fact that just like the moon during an eclipse may be still perfectly seen, so the spiral in the whorls is still recognisible by many characteristics, which will be enumerated in the Summary.

Only one of them is to be treated here: the considerable differences in developmental power of the different axillary buds in one and the same whorl. Generally only the buds of the first two leaves of a whorl may develop into side branches; and in many cases the period of size of the buds in every particular whorl is quite in accordance with the order of sequence of the leaves in the original spiral.

This phenomenon, which is quite natural as we realise that the buds of the first leaves are earlier developed and may lay hold on the whole amount of the available nutritive substances for buds, finds an analogy in the accurately regulated distribution of the developmental power of the buds in many inflorescences, which finds its highest expression in the regular composition of cymose inflorescences. The "Förderung" from α may be considered as quite the same phenomenon as we observed here; the "Förderung" from β may be only a slight variation, caused by a diminished fertility of α by a change in the period of bud formation.

The whorls here described have been termed by me binding whorls, and we have to discuss now the difference between them and the growth whorls described in my previous paper. As I pointed out in the introduction of the present paper, the chief characteristic is to be sought in the attachment of every young leaf to its two lateral neighbours. The whorl consists therefore essentially of a single row, though the leaves of the whorl originally do not stand at the same level. In the growth whorls a binding of that kind did not seem to be present; there was only a sticking together of irregular masses of leaves. In the binding whorls every leaf seems to have two places of affinity, like a bivalent atom.

The binding whorls therefore have a tendency to become isomerous, as one whorl being formed the next higher leaf primordia will unite to each other after the same parastichies, and if the connections are only formed along two sets of parastichies, the whorls can only be composed of numbers of leaves from the Fibonacci series, and so the probability of isomerous whorls may be much raised. If there are three sets of parastichies in which binding may occur other whorls may be formed too, and here a strong tendency to isomery may be the cause of the fact that the different kinds of parastichies are differently fit for the forming of new bindings, as has been elucidated in the description of *P. blanda*. In our material and in that of the Bravais a predilection for the „Fibonacci" whorls over the whorls with other numbers was really to be observed; it is however not to be followed that this will always be the case.

The most extensive record of the prevailing whorls in the genus *Peperomia* has been given by Cas. de Candolle (3, p. 192), who noted the phyllotaxis of 382 species of the genus. Of these 44 are included in a § Folia opposita, and 96 in a § Folia verticillata. Among these 96 there are 13 in which be notes: foliis ternis, 16 with „foliis quaternis" and only 3 in which he notes: „foliis quinis"; in the remainder of the species the conditions are reported as mixed, e.g. foliis ternis quaternisve, foliis quaternis-quinis etc. The high number of tetramerous species is not what we could have expected from our observations, but it is clear that our conclusions are not inconsistent with this fact. Besides it is probable that a close investigation would give many additions to the observations of de Candolle. Of our species he indicates:

P. blanda (his nr. 336) foliis oppositis quaternisve.

P. Langsdorfii (nr. 262) foliis superioribus alternis, caeteris oppositis.

P. pulchella (nr. 357) foliis ternis-quinis.

P. rubella (nr. 351) foliis 2-5-verticillatis plerumque quaternis.

In our observations the range of variability of the whorls in all four species was wider and the „Fibonacci whorls" prevailed in each of them; so in the rest of the *Peperomiae* further observations may bring many changes too.

In the introduction I gave as my impression that the binding of the primordia was a rather lax one in *Peperomia*. This impression was based on the following two reflections. In the first place the lack of any tendency to horizontal metatopy in those cases where it was not brought about by the crowding of the primordia, and the small tendency to metatopy in vertical sense. If the binding of the leaves had been very firm, growth would have met a considerable resistance in the nodes, which would likely have caused a more evenly distribution of the leaves horizontally, and which would surely tend to remove all differences in height of insertion. The second reflection was that torsions have never been reported from *Peperomia* shoots. In our cultures they never appeared, and in the litterature (2, 4, 5, 10) I did not find any mention of them: moreover, Dr. J. C. Costerus wrote to me, that he nor his collaborator Dr. J. J. Smith ever met with torsion in *Peperomia*. Of course, it may be found still, and than this reason for assuming a lax character of the binding would be invalidated; but up to the moment we may suppose that in the cases where the binding would continue after a spiral around the shoot, the growth would break the spiral easily, and the shoot would not be twisted or disturbed in any way.

A remarkable peculiarity of the whorls of our plants was the lack of any tendency to become either alternating or superposed. In all cases the divergence of the original spiral, as calculated from the whorls, was from 135° to 140°. As a consequence the dimerous whorls in this way were neither alternating nor superposed, but intermediate; the ternary whorls were as much alternating as was consistent with their differences in horizontal distances of the leaves; the tetramerous whorls were superposed; the pentamerous whorls intermediate, and the hexamerous superposed.

From the foregoing it follows that the difference between binding whorls and growth whorls is rather wide and well marked. We might now ask whether the floral whorls are perhaps related to our binding whorls. To answer this question we should have a better knowledge of floral whorls and their origin. In the predilection for 2- 3- and 5- merous whorls both kinds of whorls decidedly agree, the floral whorls differ on the contrary from the *Peperomia* whorls as they are in most cases alternating, in less but in still a good deal of cases superposed, but hardly ever intermediate. On the other hand it is possible that binding whorls in such plants, where they are formed between younger leaf primordia and where the binding is firmer, may have more marked tendencies to alternation or perhaps to superposition; further researches must settle this point. For the class of binding whorls probably will prove to be a very extensive one, embracing perhaps all plants with typical vegetative whorls, such as *Equisetinae*, *Casuarinae*, *Labiatae*, etc. etc.

In those cases we are accustomed to find alternation of the whorls; the cases of superposition are rare (*Archaeocalamites*, *Sphenophyllinae*), and intermediate cases have only been reported for some *Dipsaceae* (8, p. 168), as far as I know.

In all these vegetative whorls metatopy is much stronger, and the binding probably will prove to occur much earlier in development. In such plants investigation will still be possible in shoots, which exhibit whorls only in part of their leaves, whilst the remainder of the shoot shows at least traces of the original phyllotaxis.

§ 5. Summary.

a. In all *Peperomia* spp. observed, the phyllotaxis is of the normal Fibonacci series; in several cases the divergence seems to be about 140°.

b. In many *P.* spp. this phyllotaxis remains visible, unaltered and undisturbed.

c. In other *P.* spp. binding whorls are formed out of the spirally arranged vegetative leaves; in forming these whorls every leaf is united to its two lateral neighbours.

d. The binding of the leaves probably sets in late during the development and is rather lax. This opinion was based on the small amount of metatopy both in horizontal and in vertical sense of the leaves. If torsion of the axis really never occurs — and untill now it has not been reported — this may be a consequence of the lax coherence of the leaves.

e. As only those leaves will be "neighbours" to a certain leaf, which lie with it on the same parastichies of such a kind, as may be the contact parastichies at the moment of whorl formation. the attachments will follow in many cases only in the direction of two sets of antidromous parastichies. The consequence of it will be that 2- 3- and 5-merous whorls are formed.

In other cases the binding will be possible in the direction of three sets of parastichies, but one set of parastichies will be most fit for the origin of bindings. In those cases whorls with other numbers of leaves, as 4 or 6, will be possible.

Whether a species will product chiefly one kind of whorls or another will depend on the relative sizes of leaves and apex at the moment of whorl formation.

f. In the so formed whorls the binding causes a certain amount of metatopy in a longitudinal sense. In di- and trimerous whorls, and as far as I saw often in tetramerous whorls too, the leaves become to the eye perfectly placed at the same level; in pentamerous and hexamerous whorls there remain characteristic differences in height of insertion.

The binding may cause too a metatopy in a horizontal sense; in the dimerous and trimerous whorls we did not perceive it, but in the tetramerous it was clearly to be perceived and in the pentamerous and hexamerous whorls it was so strong as to make the leaves in the whorl horizontally equidistant.

g. In our material no tendencies to cause an alternation or a superposition of the whorls were to be observed, the position of the whorls with respect to each other was so as might be derived from an original divergence of about 135° or 140°.

h. In the whorls the original spiral may be recognised by the following means.

In dimerous whorls we observe an approachment of the leaves of every pair at one side of the stem; this phenomenon is transmitted in a secondary parastichy antidromously to the basal spiral.

In trimerous whorls we have analogous approachments ascending after a ternary parastichy, in the same direction as the basal spiral.

In tetramerous whorls one of the four distances is sometimes markedly larger than the other three; this phenomenon is transmitted in the way of a distichous phyllotaxis, so that the large space in the third whorl is right over that of the first whorl. Together with other characteristics this may betray the original spiral.

In pentamerous whorls we may have differences in the height of insertion, two of the leaves of every whorl being placed somewhat higher; the transmission of these irregularities is antidromous to the basal spiral.

In hexamerous whorls there are three higher and three lower leaves, alternating regularly in every whorl; the lower leaves of the next whorl are placed over the lower leaves of the whorl beneath, so that three orthostichies of lower leaves and three of higher leaves are to be observed. In connection with other means this may help us in establishing the original spiral.

In branching shoots only the first two leaves of a whorl in most cases give rise to a branch: these branches mostly show diminishing sizes according to the sequence of their subtending leaves in the basal spiral.

In shoots, arising from the soil the leaves of the first whorl of vegetative leaves show considerable differences in size according to their sequence in the spiral, the lowest numbers being the smallest, the following ones assuming gradually the normal shape and size of vegetative leaves.

In growing non-flowering shoots the expanding leaves diminish in size according to their sequence in the spiral.

In flowering shoots the last vegetative leaves under the inflorescence even when full grown show diminishing sizes according to the same sequence.

i. The only prophyll or the two prophylls of every lateral shoot are placed laterally; the basal spiral starts from the first of them and runs opisthodromously to the second prophyll or to the first leaf. The first leaf of every shoot is therefore placed either nearly opposite the only prophyll, somewhat backward, or when there are two prophylls, at the frontside of the shoot, nearer to the first prophyll.

In those cases where there is only one prophyll the direction of the basal spiral is, in consequence of what has been said, left-handed after a prophyll at the right and inversily.

j. The bracts in the inflorescence are formed according to the same phyllotaxis as the vegetative leaves, and as the whorl-forming factors do not prevail there, the normal phyllotaxis comes again to light, the direction of the basal spiral being the same as in the vegetative leaves.

k. The lateral branches of *Peperomia*, though being formed in the axils of whorled leaves, have a certain tendency to be antidromous to their main axis, this furnishing a new argument for the real existence of a spiral in the whorled part.

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