ON COROLLA AESTIVATION AND PHYLLOTAXIS OF FLORAL PHYLLOMES

BY

J. C. SCHOUTE

CONTENTS

INTRODUCTION.

"Die Aestivation ist ein gefährliches Irrlicht für den unerfahrenen Wanderer auf dem Pfad der Taxologischen Untersuchung! Ihre Täuschungen und zugleich ihre Gesetze aufzudecken wäre nichts Geringes und nichts Leichtes" (BRAUN, 1, p. 291).

Any doctrine of phyllotaxis should of course not only consider the vegetative leaves, but also all other leaves, including the floral phyllomes, and should study their spatial relations.

When in most works on phyllotaxis the vegetative region of the plant is treated almost exclusively, this is not due to any disregard for the phenomena to be observed in the floral region, but only to the consideration that the vegetative region is less complicated in this respect and therefore offers a better opportunity for solving the general problems.

Having myself given in former years a theory of phyllotaxis, I often pondered on the facts of floral phyllotaxis, and always gathered them where I could. Among these facts there is one special group which is perhaps most stimulating and inviting for research, namely the peculiar mixture of spiral and whorled phyllotaxis. The proper nature of this mixture has often been treated from several points of view, but we may say that even a plausible conception of a possible explanation still remains to be fulfilled.

The aim of the present paper is now to show that it is possible to include this field in the ordinary conception of a general phyllotactical theory without any extravagant suppositions.

As the domain of floral phyllotaxis is extremely wide, I have chosen for my researches a limited part of it, namely the aestivation of the Dicotyledonous corolla. This choice may be justified by the remark that the corolla is the first floral belt with the typical floral whorl formation. The calyx is in its phyllotaxis more akin to the vegetative region and therefore does not present so many of the particular points in question.

For a thorough treatment of the subject it is necessary to base the research on a large body of facts, to be gathered from literature as well as from direct observation.

I shall therefore come to the following division of my paper.

CHAPTER 1. *Current ideas from literature on the phyllotaxis of floral phyllomes.*

CHAPTER 2. *Facts about corolla aestivation from literature.*

CHAPTER 1.

Current ideas from literature on the phyllotaxis of floral phyllomes.

According to most botanists the floral phyllomes of Dicotyledons are in the majority of cases placed in whorls, and only in a few cases have we plants with a continuous spiral order of all floral parts, as e.g. *Calycanthus*.

A closer examination reveals however that in a considerable number of the Dicotyledons we have no perfect whorls but intermediate conditions between spiral and whorled arrangements. These intermediate conditions show so many grades that we may arrange them in an uninterrupted scale of gradual transitions between the two extremes.

In the pure spiral form the different belts have an undetermined number of members and the limit between the successive organ categories is not a sharp one. The first step towards the whorled condition is the limitation of the number of members, in such a way that as far as possible the members are placed evenly on all sides of the flower; this end is gained in the simplest way by limiting the number to one of the figures of the main series as 3, 5 or 8.

At the same time the limit between the successive belts usually becomes very sharp; the formation of the false whorl has been "scharf abgesetzt", sharply marked off. The spiral order may be recognized however from the difference in the insertion level, from the secondary divergences, and from the aestivation.

The next step is that the members of the whorl become more or less equidistant. If equidistance has been fully realized, the aestivation may reveal the original spiral perfectly well, at least in trimerous or pentamerous whorls. In tetramerous and hexamerous whorls this test no longer serves, as the characteristics of the aestivation of false whorls with these numbers of members coincide with those of true decussation and of alternating trimerous whorls.

This stage is the common one in the Dicotyledonous calyx. Most botanists recognize the spiral nature of the calyces with an odd sepal number, whereas those with an even number are taken as truly whorled.

In the corolla the whorled formation has become much more complete. Cases where the corolla is not strictly delimited are very rare because only fully spiral flowers have no clear distinction between calyx and corolla, as *Calycanthus* and the *Cactaceae*; in *Nymphaea* we have further a case where the corolla has no sharp delimitation towards the stamens.

Cases of well-limited corollas with an evident spiral character are rare;

the families of the *Ternstroemiaceae* and *Hippocrateaceae* forming good examples,where the developmental sequence as well as the aestivation is eutopically spiral.

In the majority of cases the corolla shows no traces of a spiral origin, and even the aestivation does not furnish any indication; these cases are usually considered as truly whorled.

Stamens and carpels with a clear spiral arrangement are still more exceptional and may only be found in wholly spiral flowers like *Caly-canthus* and in some *Ranunculaceae*.

The facts of these transitions deserve our full attention; they point undoubtedly in the direction of a transformation of whorls into spirals or spirals into whorls.

Another equally remarkable fact is that the calyx spiral, even when weakly expressed, always forms the continuation of the phyllotaxis of the lower phyllomes of the floral cormus: in terminal flowers it continues the phyllotaxis of the foliage leaves, in lateral flowers that of the prophylls. This makes it more or less probable that the relation between spiral and whorl will turn out either to be caused by a change of spiral phyllotaxis into whorls by metatopic displacements, or that we have to accept some conception of true whorls in which a spiral tendency of lower phyllomes may more or less retain its influence and may gradually die out.

Both these opinions have been explicitly enounced in literature, we meet with the former idea in the works of VON MARTIUS, SCHIMPER, BRAUN, WYDLER and EICHLER; the second opinion has been expressed exactly in the above form by HIRMER.

Other authors more or less disregard the gradual transitions between whorls and spirals and take for granted that any whorl without traces of a spiral origin must be a real whorl; AD. BRONGNIART, CHURCH, GOEBEL and REINSCH may serve as examples.

In more than one case the authors derive part of their arguments from the corolla aestivation; a somewhat lengthy consideration of the facts brought forward by these authors may follow.

The eldest of the above authors, VON MARTIUS, does not need to detain us very long. In 1828 he takes all floral whorls as being properly spirals (32, col. 523) and he bases his opinion on a typical "naturphilosophisches" comparison between floral whorls and the circulation of the animal organisms, and with the cosmical laws.

It is only a few years later that we find the same view, but with quite another and much better argumentation in the writings of SCHIMPER and BRAUN. SCHIMPER bases himself in 1829 on the conception of the floral parts as metamorph leaves which are kept together in periods (40, p. 82); the pentamerous calyx with a quincuncial aestivation is especially brought forward. These periods appear as natural wholes, they keep themselves apart from other periods and give place to other periods in the same manner as a single leaf does to other leaves.

Without doubt the deeper ground for SCHIMPER's conviction is his conception of the formation of phyllomes as an undulating movement at the vegetative cone, or as he called it a "caulophyllogonische Wogung" (33, p. 171); this conception has commonly be looked upon as a consequence of the "Naturphilosophie" of those days, but we should rather take it as a physiological hypothesis, which has not been confirmed later on.

BRAUN writes (33, p. 282) that for a long time he thought that possibly all spirals might originate by the solution of whorls. In his "Tannenzapfen" he treats this question at great length (1, p. 341—354) and brings forward an astonishing amount of excellent observations. The chief argument inducing him to believe that all whorls are contracted spirals, in the flower as well as in the vegetative region, is supplied by the dispersions which occasionally occur in all whorls, and the phenomena to be observed in such cases.

Here we meet for the first time the corolla aestivation. In view of BRAUN's much-embracing knowledge of morphological facts it is but natural that he mentions the overlapping of the petals and that he compares it with the postulated spiral order. On finding that the observed order of overlapping is quite different from what might have been expected from the spiral order of the sepals, he does not conclude that the petals do not continue the calyx spiral, but he only comes to his judgment of the aestivation as being a dangerous Will o' the wisp, which I quoted above as a motto. He expounds further: "Die Aest. imbricativa ist bei der Blume fast immer triegerisch, beim Kelch zwar zuverlässiger, aber in manchen Fällen dennoch täuschend, also dass es schwer ist, zu entscheiden, wann mann auf sie bauen darf; die Aest. contorta setzt einen Schein von Succession und hebt ihn selbst wieder; wenn endlich die Aest. valvaris aller Succession widerspricht, so traue man ihr so wenig, als den beiden vorigen" (1, p. 292).

Such a neglect of obvious facts may easily give an impression of obstinately clinging to preconceived ideas and such a seemingly unscientific attitude without any doubt often has affected the appreciation of morphology in botanical circles. Against a man like BRAUN we should however always be very cautious in our judgment, as he based his opinions on an unparalleled knowledge of facts, and he often did not bring forward all his arguments. In the present case I hope to show that BRAUN was quite right.

In the same year 1831 ADOLPHE BRONGNIART published a special paper (8) on floral phyllotaxis, a paper which even mainly treats with the calyx and corolla aestivation and in which the author is inclined to take the aestivation as the best proof for the original phyllotaxis. All cases of valvate and contort aestivation are considered as indicating true whorls, in this respect differing from BRAUN.

All cases however of imbricate aestivation, whether quincuncial,

descendent, ascendent or any other form, are taken as proof of a normal spiral phyllotaxis. No arguments being given for this opinion which has been upheld much better a few years later by the BRAVAIS brothers, we may postpone the discussion of it here.

The next authors to be quoted, WYDLER and ROEPER, being of the school of AL. BRAUN, absolutely shared his opinion that all floral parts are placed in a spiral. WYDLER writes about the aestivation of a leaf complex in general: "die Deckung...... entspricht entweder der genetischen Folge der Blätter, oder sie ist von ihr unabhängig" (62, p. 121).

Consequently he distinguishes between eutopic and metatopic aestivation of which he cites numerous instances.

And ROEPER, describing the strongly varying corolla aestivation of *Pirola minor* of which he found 17 different forms in 37 flowers only remarks that it furnishes "ein neuer Beweis von der Unzuverlässigkeit der Ästivatio um die wahre Aufeinanderfolge der Blumenorgane zu ermitteln" (39, col. 431).

The common opinion of all these authors, even though based on so many alleged facts and arguments, was predestined to fall from favour with the new rationalistic school, founded by SCHLEIDEN and fully developed by HOFMEISTER, for whom the whole spiral theory was too idealistic, too much of a spiritual product of the detested "Naturphilosophie".

In his Allgemeine Morphologie HOFMEISTER wrote: "Die Vorstellung vom schraubenlinigen oder spiraligen Gange der Entwickelung seitlicher Sprossungen der Pflanzen ist nicht bloss eine unzweckmässige Hypothese; sie ist ein Irrthum. Ihre rückhaltlose Aufgebung ist die erste Bedingung zur Erlangung eines Einblickes in die nächsten Ursachen der Verschiedenheiten der Stellungsverhältnisse im Pflanzenreiche" (26, p. 482).

In itself this criticism doubtless was just. The conception of a spiral wave motion at the vegetative cone does not correspond to the facts and the theory of junction, proposed by HOFMEISTER instead of it, is an ingenious conception which has since formed the basis of nearly every phyllotactical theory.

Yet we may say from a more general point of view that the criticism HOFMEISTER applied to the idealistic morphology was erroneous and one-sided, and that this attitude has inflicted very serious damage on the morphology owing to the great influence HOFMEISTER exerted on his contemporaries. Indeed HOFMEISTER, great as he was, not only suffered from his famous obscurity, but from other serious faults as well.

One-sided was the criticism because he ignored many of the important facts discovered by the exertions of the old school, facts which in more than one detail would have immediately invalidated some point of his arguments.

With the over-estimation which was proper to the whole experimental natural science of his time he thought that the developmental observation

of morphological facts was a near approach to a direct research on the mechanical causes. The developing primordia on the vegetative cones with their strained outlines were taken as the first stages of the later organs, showing all their properties, as if they were distended water-bags instead of meristems with a whole world of substances and forces in their protoplasm.

It was exactly by this over-estimation that HOFMEISTER believed — and following his example many botanists have believed it up to the present day — that developmental research does furnish us with the means of an examination of the mechanical causes of morphological phenomena, and that it was therefore no longer necessary to pay attention to the works of the older morphologists who had "only" studied the adult forms by the comparative method and piously described the plants as products of unrevealed laws.

To realize the impression HOFMEISTER's Morphology made on AL. BRAUN, it is sufficient to read BRAUN's letter of March 9th 1869 to his friend IRMISCH and his letter of April 10th of the same year to DESCAISNE (33, p. 676), in which he mentions the fright given to him by the book and the uncredible things brought forward without a due comparative base.

As to our topic, the floral phyllotaxis, HOFMEISTER had repudiated the wave-motion of SCHIMPER. But the fact of the transitional forms between spiral and whorl remained unimpaired and his conclusion that the corolla in general is truly whorled remained premature, so that in morphology the idea was not abandoned that floral whorls may be formed out of spirals by metatopy.

This is clearly proved by EICHLER, the man who tried to reconcile the idealistic and the rationalistic schools, and tried to unite the modern physical and chemical habit of thought to the real results of the old morphologists, of which he possessed a vast knowledge.

Consequently he started with the trial of taking all floral whorls as a "thatsächliches und ursprüngliches Stellungsverhältniss" (17, I, p. 15); not by lack of appreciation of the transitions between whorls and spirals, but from his desire to stand wherever possible on the solid foundation of empirical knowledge and to avoid every unnecessary speculation. The simultaneous origin of the petals seemed to him a sufficient ground, even though developmental history were not always a trustworthy guide (17, I, p. 15).

Later on he was however obliged by the facts to abandon this opinion and to return to the views of SCHIMPER, BRAUN and the BRAVAIS' (17, II, p. XIV): "Es mag demnach doch die Ansicht haltbar bleiben, wonach die Quirle zusammengezogene Spiralen darstellen".

The argument turning the scale for him was furnished by the fact that some corollas, clearly originating in a quincuncial order and with a quincuncial aestivation in the adult condition, were yet found to alternate with their calyces. Hitherto he had been under the belief that alternation

belonged to the whorled condition and that in a pentamerous spiral flower the corolla should be superposed to the calyx; this difference had been his last hold-fast.

That EICHLER did not consider the developmental history as decisive in morphological questions appears also from several other places of his "Blüthendiagramme", e.g. from his judgement of the value of aestivation for the determination of phyllotaxis (17, I, p. 29).

There is, further, one statement in EICHLER's work which we shall have to consider more in detail, though EICHLER himself did not bring it forward in connection with the question of whorl or spiral in the flower, namely the aestivation of the perianth in the family of *Portulacaceae,* including the *Basellaceae.*
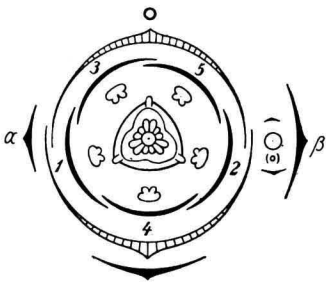
For the reader's convenience I reproduce here in fig. 1 a diagram given by EICHLER for *Calandrinia procumbens.*

On the two prophylls, of which β is fertile and often inserted at a higher level, there follows a dimerous involucre the anterior bract of which overlaps at both edges. After these two pairs of decussate phyllomes the pentamerous perianth follows with a clear quincuncial aestivation.

Fig. 1. *Calandrinia procumbens;* case with five stamens. From EICHLER (17, II, p. 125, fig. 47A).

For EICHLER this perianth aestivation does not present a question at all; the spiral following on the decussation may have any course. When however we take all cases of decussate phyllotaxis in Dicotyledons as transformed spirals in which the phyllomes have been placed by metatopy in opposite pairs (47), the case changes altogether.

Then the spiral of the perianth must be the continuation of the spiral hidden in the foregoing phyllomes. In our fig. 1 we easily see that this is not realized here: the perianth spiral should start from tepal 2, not from 1, and should run in the opposite direction.

This might therefore be a serious argument against the whole spiral phyllotaxis of the flower. It is for that reason that I have examined a number of species from the families mentioned above and instituted a special investigation on that point. For the details I refer the reader to that paper, to be published soon; I only want to say here that the results were such as to prove that there is no objection whatever against the spiral phyllotaxis in these facts.

When we now proceed to the later morphologists, after EICHLER, we shall find different opinions about the floral phyllotaxis; some authors more or less adhere to opinions like that of EICHLER but partly in a weakened and ill-defined form; others, with HOFMEISTER, take the floral whorls as an original condition, partly however on grounds quite different from those of HOFMEISTER.

PAX for example declares that in cyclic flowers the spiral has been interrupted by the union of a certain number of phyllomes into a whorl (34, p. 169); repeatedly however he emphasizes that the derivation of whorls from spirals is to be conceived as a phylogenetic process (34, p. 67, 169), introducing in this way quite a new element into the conception, as it is evident that a whorl, though phylogenetically derived from spiral phyllotaxis may yet be formed ontogenetically as a whorl.

The same point of view, only more pronouncedly, is held by ČELAKOVSKY who declares that the transition from spirals to whorls is "nicht so zu verstehen, als ob alle Blüthen der jetzigen Pflanzenfamilien und Gattungen spiralig gewesen und erst mit der Entstehung der Familie und Gattung cyklisch geworden wären; für die meisten Familien, die nur cyklische Blüthen besitzen, hat schon anfänglich ein cyklischer Blüthenbau bestanden, nur für weit zurückliegende Urahnen ist spiralige Anordnung anzunehmen" (14, p. 51).

I do not want to contest this opinion; but I have to remark that a phylogenetic derivation is quite another thing from an ontogenetic one. In the present paper it is only the last mentioned derivation that interests us; the difference between these two conceptions has not always been duly represented.

VELENOVSKÝ writes about our point in view that we must "jede vollkommen cyklische Blüte als eine zusammenhängende Spiral ansehen, welche sich in Abteilungen von gleicher Anzahl, die uns die einzelnen Cyklen darstellen, zerrissen hat" (57, p. 846); it is however not clear whether this must be understood phylogenetically or ontogenetically. From the context of the paragraph I am inclined to believe that it has been meant more phylogenetically than ontogenetically.

Of the authors who take the floral whorls as true whorls I want to quote CHURCH in the first place. The difference between whorl and spiral is for him a question of symmetry: a symmetrical growth is the condition for whorled phyllotaxis, asymmetrical growth for spiral. CHURCH too derives the whorls phylogenetically from spirals: "Primarily, then, it may be said plants possess asymmetrical growth as a necessary consequence of the limitation of new members to serial succession of individual units, and that the symmetrical condition, in which new cells are added at the apex in all directions contemporaneously, is a secondary phenomenon. evolved as a distinct improvement on the older method" (15, p. 36); the idea that spirals when laid out might be converted by metatopy into whorls, would not fit in with his conceptions.

This view, when applied to flowers, brings the consequence that the symmetrical construction is incompatible with any kind of imbricate aestivation: "no sliding effect is allowed for in the primary construction: such members should exactly and symmetrically meet at their edges (16, p. 185)...... and conversely a valvate prefloration affords suggestive evidence of symmetrical construction" (16, p. 186).

That this extreme stand-point is not in conformity with the natural conditions, follows immediately when we take into consideration that the calyx of the *Columniferae* with its valvate aestivation has been found to arise in all families of the group in a quincuncial order, and that moreover the contort corolla of the same plants for the direction of its contortion depends upon the direction of the calyx spiral, as the BRAVAIS' already knew.

Putting this objection for a moment aside, we must remark that the explanation, if one wants to call it so, is quite another from that given by HOFMEISTER. It is not the junction of the newly formed phyllomes to the older ones, but the symmetry that is made responsible for the resulting form. So we leave the field of physiological conceptions to embark on ideas of a "naturphilosophisches" kind; for an inner principle would control the outer form in an incomprehensible way.

The same point of view is taken by GOEBEL in some of his works. Thus he writes in 1913 about whorl formation: "Sie tritt dann ein, wenn das embryonale Gewebe dauernd eine symmetrische Beschaffenheit beibehält, während "spiralige" Blattstellung stets durch asymmetrisches Verhalten des embryonalen Gewebes bedingt ist" (21, p. 197); on the same page he writes further that an inner principle controls the uniform distribution. Later, in 1923, he writes that the cyclic flower arises from the acyclic by "Änderung in der Gesamtsymmetrie des Blütenvegetationspunktes (der, bildlich gesprochen, aus einem gedrehten zu einem geradläufigen werden muss)" (21, p. 1569).

In other places GOEBEL mentions however another cause for the occurrence of spiral phyllotaxis, namely the spirotrophy, i.e. "eine Förderung der Baustoffzufuhr in der Richtung einer Schraubenlinie" (21, p. 202, further ibid. p. 196, 212; the first mention of the term seems to have been in 1908 (19, p. 153).

With this spirotrophy we come back to the physiological sphere of ideas, though in an ill-founded and improbable way. As compared with SCHIMPER's "caulophyllogonische Wogung" the spirothophy is not to be called an advance; at the utmost a revival in a different, but quite as out of date guise.

And on a third occasion, in 1913 (20), GOEBEL gives a description of the false whorls of *Peperomia* which he declares do not arise from a spiral, but from pairs of opposite leaves.

I must confess inability to follow these lines of thought, the more so as in more than one case assertions take the place of arguments.

The last authors whose opinion I want to refer to are M. HIRMER and his pupil M. BREINDL.

HIRMER shares the wide-spread opinion that most flowers are truly whorled; he not only takes most dimerous, tetramerous and hexamerous as whorled but moreover most trimerous flowers too (25, p. 198). It is only

the calyx in many pentamerous flowers which is spiral and moreover a very few flowers are spiral throughout in all their phyllomes.

The underlying cause for the appearance of the whorled condition in flowers is a change of the basal symmetry type; hereby the distribution of formative substances is altered and new phyllomes only may be laid down in whorls.

In the calyx however a mixed condition often ensues which may even extend in some cases into the androecium.

Such a conception of a gradual dying out of the spiral influence in a truly whorled phyllotaxis evidently does not meet with any objection from an idealistic point of view, when we take the symmetry principle as a morphogenetic force.

When we try however to explain the phenomena of phyllotaxis on a line of thought which is customary in natural science and especially when we follow HOFMEISTER in his idea of the ontogenetic elaboration of every phyllotaxis system by junction of the younger phyllomes to the older ones, the whole conception becomes untenable.

More important for our purposes is that HIRMER brings a number of observations on the secondary divergences of floral members. Starting from his belief that in spiral phyllotaxis, at least in that of the Dicotyledons, the irrational limiting angle is the only divergence realized in nature, he expects to meet with this same angle in flowers too.

He succeeds in stating that in a number of Ranunculaceous flowers of admittedly spiral character the organs of the same plastics, whether they are 3, 5, 8 or any other figure in number, are never equidistant but that they show larger and smaller interstices such as may be expected from his point of view.

He further puts the question what may be found in a spiral calyx of an otherwise whorled flower, and he states that at least in *Datura* there are two smaller and three larger interstices at the required places; the same result moreover is reported by BREINDL (9) for *Linum* and other plants.

These observations may surely be useful for our conceptions about floral phyllotaxis. They are not absolutely new, as it clearly appears from the statements of the BRAVAIS brothers (5, p. 75, 6, p. 210, 7, p. 37) that they were strongly opposed to BRAUN's statement of any $2/5$, $3/8$ or $5/13$ phyllotaxis in Ranunculaceous flowers as well as in calyces of other Dicotyledons; on the contrary they claimed the presence in all these cases of irrational divergences of the limiting angle; the merit of the observations by HIRMER and his school however is that they have furnished us a better basis of controllable and well defined facts.

If their observations are confirmed[1]) they may give new evidence of

---

1) In some cases some doubt may be allowed as to the general validity of their conclusions. In his figure of DATURA (25, fig. 110, p. 198) HIRMER pictures a pentamerous androecium with two small and three large intervals, and he concludes on an influence

the spiral in parts which always have been recognized as having it already, by taking into account another characteristic, namely that of the secondary divergences.

Summarizing we may say that a number of authors follow SCHIMPER in believing that all flowers originally are spiral, but that more or less perfect false whorls may be brought about by metatopies.

HOFMEISTER on the contrary only recognizes the junction to the lower phyllomes as the cause of phyllotaxis. So he rejects the spiral in nearly all flowers; the fact of the transitions between spiral and whorl is not taken into account and the frequent occurrence of floral whorls, which would constitute a great difficulty for any pure junction theory is passed by in silence.

Finally a third group of authors tries to explain the arrangement of floral phyllomes by conceptions without a physiological background, like phylogenetic changes, principles of symmetry or spirotrophy; all these conceptions will be left out of consideration in the present paper.

---

of the spiral tendency continued into the androecium. The approached pairs of stamens however are not the numbers 11 and 14, and 12 and 15, as a continued spiral would require, but 12 and 14, and 13 and 15; pairs which should have large intervals in between.

The different intervals in this individual flower must have been due therefore to another complex of causes.

CHAPTER 2.

Facts about corolla aestivation from literature.

The knowledge of aestivation before 1829 was mainly restricted to the description of its different modes and the application of these distinctions in plant taxonomy.

At the same time technical terms were framed for these different modes. The question of this nomenclature was often treated at considerable length; in the present paper this will be left aside and I shall only give my own set of terms in the next chapter.

The first authors dealing with aestivation in a more scientific way, with a keen interest in the subject itself, were SCHIMPER and BRAUN: in Chapter 1, I have already made mention of the proper valuation of the quincuncial calyx by SCHIMPER in 1829, and of the observations and reflections of BRAUN in 1831.

Before dealing with the important results obtained by BRAUN from later investigations, the chronological order brings us to the paper by BRONGNIART, referred to already (8).

In this paper namely we find not only the views about floral phyllotaxis, quoted above, but moreover a developmental study of the origin of the corolla aestivation. These observations, though perhaps the first ever instituted on the topic, are so thorough that they reveal nearly everything which is known of it at the present day.

Having observed that for a long time the corolla is much behind in its development with regard to the other floral parts, he writes: "On voit donc que la corolle étant à cette époque plus courte que les étamines, les lobes ou les pétales ne peuvent pas encore se recouvrir, et que ce n'est que par suite de leur développement que leurs bords s' atteindront et pourront se recouvrir. Si leur développement est régulier, si rien ne vient intervertir leur disposition naturelle, ils se recouvriront dans l'ordre de leur insertion, le plus inférieur se trouvant le plus extérieur; mais si leur développement est inégal, ou si les étamines les soulèvent irrégulièrement, leur mode d'imbrication pourra être modifié.

Si un des pétales prend un accroissement plus rapide que les autres, il s' appliquera immédiatement sur le sommet des étamines et sera ensuite recouvert par les autre pétales qui se développeront plus tard. Il en résulte que fréquemment, dans les fleurs où les pétales prennent un accroissement inégal, ce sont les plus grands qui sont placés en dedans et les plus petits en dehors. C'est ce qu'on observe dans les Personnées et les Labiées......

On voit par là que la tendance des pétales à se développer inégalement rompt les rapports naturels qui existaient dans leur mode d'imbrication et ne permet plus de juger de leur ordre d'insertion autour de l'axe : en effet, dans les fleurs irrégulières, si on voulait déduire l'ordre dans lequel les pétales sont fixés sur l'axe de la fleur, de la manière dont ils se recouvrent, comme nous l'avons fait pour les fleurs régulières, on trouverait un mode d'insertion qui ne serait plus ni une spirale ni un verticille, qui en un mot, n'aurait aucune analogie soit avec l'insertion des mêmes parties dans les fleurs régulières très-voisines, soit avec l'insertion des feuilles sur les rameaux'' (8, p. 230).

As we see BRONGNIART renders full justice to the late appearance of the corolla aestivation as well as to the many disturbing factors which may influence it.

The curious result of the earliest developing petals becoming wholly overlapped, has been obtained again independently nearly a century later by REINSCH (36); the reliability of the observation is therefore beyond doubt.

Shortly after, in 1837, the BRAVAIS brothers published their brilliant paper on the inflorescence (6) in which they deal with aestivation too.

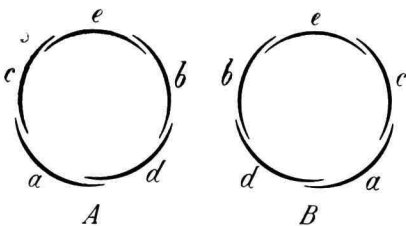Though fully recognizing that the aestivation may be a very imperfect reflection of the original spiral (6, p. 218), they contend that not only is the quincuncial calyx aestivation due to the original calyx spiral, but that in the same way the cochlear aestivation, and even the valvate and the contort aestivation are to be taken as derivated forms of the original spiral.

Fig. 2. *Cercis Siliquastrum*. Corolla aestivation after the BRAVAIS brothers (6, pl. 8). The five petals have been indicated as *a — e* according to the genetic spiral; in the median plane *a* always overlaps *d*.

They begin their argumentation with a very remarkable observation on the cochlear aestivations, of which they say that they are, ''comme le quinconce, susceptibles de deux formes différentes, la forme dextrorse et la forme sinistrorse, liées avec le sens de la spire pédonculaire : ainsi dans le *Cercis Siliquastrum*, si la spire pédonculaire est dextrorse, l'estivation involute'' (i.e. ascending) ''aura la forme (fig. 13), et dans le cas inverse nous aurons la forme contraire (fig. 13 *bis*)''. For the reader's convenience these figures are reproduced here, 13 as fig. 2A and 13 *bis* as 2B. ''L'on retrouve donc ici l'influence de l'ordre spiral sur l'estivation, et probablement cette cause réside dans la spire génératrice pédonculaire.''

This important fact which I can wholly confirm, tells us that whereas the aestivation of the corolla is wholly ascending, no doubt in connection with the prevailing zygomorphy, there is still one corolla edge, situated

in the symmetry plane, where the aestivation remains strictly eutopic and changes with the calyx spiral. I shall come back to this fact in Chapter 6, but want to remark already here in anticipation that in this way a most valuable and important characteristic of the spiral phyllotaxis is brought to light.

Turning then to the cases of the valvate and the contort corolla the authors continue: "Nous croyons de plus que les estivations valvaire et contournée doivent encore se rapporter au même type. N'existe-t-il pas des Caryophyllées gamosépales et valvaires à côté d'autres polysépales et imbriquées? des Solanées et Borraginées gamosépales à côté des *Petunia* et des *Cerinthe*, des Personées Acanthacées et Labiées à estivation quinconciale (*Digitalis, Scrophularia, Justicia, Betonica*, etc.) à côté d'autres dont l'estivation est indistincte? Et dans le même genre (*Andromeda, Echium*) certaines espèces ne sont-elles pas quinconciales et d'autres valvaires? On ne peut guère admettre que des formes calicinales essentiellement différentes existent dans les plantes d'une affinité si marquée. Si donc l'un de ces deux états est une dérivation de l'autre, c'est l'état valvaire qui doit être subordonnée au quinconce, et si ce dernier n'était qu'une anomalie de l'autre, on ne verrait pas pourquoi la spire calicinale serait toujours exactement la continuation ascendante de la spire du pédoncule. En admettant notre théorie, il est facile de concevoir l'estivation valvaire: l'état gamosépale de certains involucres de Composées (*Tagetes, Helminthia* etc.), la comparaison de l'involucre trifide des *Lavatera* avec l'involucre triphylle et spiralée des Mauves seront des inductions de plus en sa faveur. Enfin sur l'*Hypericum perforatum*, si la spire pédonculaire est dextrorse, l'estivation de la corolle est contournée *dextrorsum*, et elle l'est *sinistrorsum* dans le cas contraire" (6, p. 217).

Their last quoted sentence conveys the curious fact that the corolla contortion direction may depend on the calyx spiral direction; a fact of considerable theoretical interest which was entirely new at that time.

Only BRAUN undoubtedly knew it from his unpublished observations; in January 1833 he wrote to NEES AB ESENBECK that he had been collecting many observations on aestivation (33, p. 254) and in 1838 he read a paper in Freiburg (2, p. 311) in which the same fact was not only reported independently, but moreover was united with a great number of similar and analogous facts into a completely elaborated system.

BRAUN found namely that there are two kinds of contort corolla aestivation, "entweder nämlich ist die Drehung *selbstständig* (von keiner andern Beziehung abhängig) und alsdann *beständig* (in allen Blüthen gleich), oder die Drehung ist *von der Blattstellung* abhängig (und zwar stets dem langen Weg der Blattstellung folgend) und in diesem Fall *wechselnd* (nach der Wendung der Blattstellung verschieden)" (2, p. 311).

Examples of independent contortion are enumerated: *Gentianeae, Asclepiadeae, Nerium* and other Genera of *Apocyneae*, further *Dianthus,*

Saponaria and *Gypsophila*, all with constant right contortion; *Vinca* and other genera of *Apocyneae* with constant left contortion; constant contortion is moreover reported for *Myosotis* and the zygomorphic flowers of *Ruellia*.

As examples of varying contortion he mentions the families of *Lineae*, *Oxalideae*, *Geraniaceae* (partly), *Malvaceae*, *Hypericineae*, *Cistineae*, the genera *Lychnis* and *Silene*, etc. (2, p. 312).

With the exception of the changing corolla aestivation of *Hypericum* which had been reported the year before by the BRAVAIS' as we saw, all these facts were entirely new.

Some years afterwards BRAUN gave a new and better system of the *Sileneae* (3), based on the difference in contortion. This system has been maintained up to the present day. But otherwise we may say that botanists have paid remarkably small attention to the important difference in the way of contortion. Not only has nobody ever seemed to have pondered about the causes of this curious set of facts, but the facts themselves have been almost completely forgotten.

This may be partly BRAUN's own fault in so far as he had simply described the facts without framing a couple of impressive learned terms; but the principal cause of the oblivion is to be sought for in the fatal influence of HOFMEISTER's school.

In 1847 IRMISCH described the foliatio corollae for many *Scrophulariaceae* (27, col. 81) and several plants of related families. He found the descendent aestivation in most *Antirrhineae*, whereas he mentioned for the *Rhinantheae* that the "beharrlich wiederkehrende" relation is the overlapping of the lateral lobes of the lower lip; in a second paper (28, col. 641) he added numerous statements of similar aestivations in *Labiatae*, *Solaneae* and other families.

In 1850 WYDLER published his important paper on the foliar aestivation (62) in which a great number of accurate observations is brought forward. BRAUN's results on the contorted corolla are confirmed[1]) and the number of examples is enlarged; further WYDLER gives numerous instances of eutopically quincuncial corollas.

In the same paper WYDLER describes the connection between the position of the symmetry plane and the aestivation of zygomorphic corollas, a connection which, as far as I know, no botanist ever had paid attention to before.

As he had described previously (61, col. 609) the symmetry plane usually coincides with the median plane, but in a number of cases its position may be different, so that it forms a certain angle with the median plane.

The corolla aestivation (and often the calyx aestivation too) follows

---

[1]) According to his usual wont WYDLER does not mention BRAUN's paper; see my paper in commemoration of the fiftieth anniversary of WYDLER's death (46).

the position of the symmetry plane, as either the back petals are overlapping (descendent aestivation) or the front petals overlap (ascendent aestivation), or the two lateral petals overlap, as reported by IRMISCH. Not only are these facts new, but the technical terms ascendent and descendent are given here for the first time, and may have been devised by WYDLER, or they may perhaps come from the same source as most morphological terms, namely from CARL SCHIMPER.

It is hardly necessary to mention that WYDLER cites numerous examples of these aestivations; further he expressly states, as was to be expected, that all the aestivations are metatopic.

Shortly after WYDLER's paper WICHURA published his treatise on the twisting of leaves (60) in which a wealth of observation is given in a systematic order. WICHURA also treats the contort aestivation and puts the question whether it is the consequence of a twist of the petals or conditioned by a skew insertion of the petals.

WICHURA adopts the first supposition and gives two arguments for it. In the first place a skew insertion should not only be discernible in the free corolla of a sympetalous corolla, but should find its expression also in the tube; or properly a skew insertion should prevent the connation of the petals.

In the second place — and this argument is considered as conclusive — WICHURA finds in a *Helicteres* sp. a case in which the claw of the petals is provided with a tooth at both sides, and he observes that these teeth overlap each other in a contort manner, but antidromously to the contortion of the limbs, so that in a right contort corolla the teeth are left contort.

This result can never be brought about by skew insertion: an opposite twist in the lower and in the higher parts of a leaf on the contrary is of very common occurrence, as follows from his numerous instances (60, p. 66).

After this paper of WICHURA we may say that our knowledge of the corolla aestivation has not made any real progress.

Of course EICHLER has collected in his usual detached and thorough way the whole material of facts from literature and from his own numerous observations, and has given a clear survey of them, arranged according to the natural families. Anyone wanting to get some information on the aestivation of a given plant, will therefore look up his "Blüthendiagramme". But EICHLER never proceeded to general considerations of the aestivation, never gave his general views, excepting his opinion that the aestivation may be easily influenced by secondary causes (17, I, p. 29).

It is only in one respect that EICHLER gives something less than BRAUN. As mentioned above BRAUN had stated that the changingly contort corolla was always twisted according to the long way of phyllotaxis, and WYDLER confirms this statement.

In EICHLER a general statement is lacking: he only denotes for all

instances, given by BRAUN or by WYDLER or observed by himself: "Krone convolutiv nach KW der Kelchspirale" which is the same statement in his terminology. But in one single case, that of *Statice,* EICHLER writes: "in den successiven Blüthen wechselwendig nach dem langen Wege der Kelchspirale (Fig. 168 A)". (17, I. p. 329). In his terminology this is the reverse relation: EICHLER however passes silently over this exception, which would certainly be very remarkable and very important for any future explanation of the contortion.

We might therefore think of a slip of the pen, a copying of WYDLER's statement (65 p. 39) without changing the reverse terminology, if the fig. 168A, the diagram of *Statice,* did not clearly indicate the unusual relation.

As the occurrence of a single well established case of a changing contortion in the opposite sense from the usual cases, would present the most serious difficulties to the explanation of this kind of contortion to be brought forward in Chapter 4, I have taken great pains to establish the real state of things; I have therefore studied the plants themselves as well as the available evidence from literature.

This last source made it already very probable that EICHLER was wrong this time in his text as well as in his diagram — quandoque bonus dormitat HOMERUS — and that *Statice* yet falls in line with all the other cases.

In the first place we have the statement of WYDLER that *Statice* in its corolla is contort "nach dem langen Weg der vorausgehenden Blattspirale" (the normal condition, in his terminology). This place is cited by EICHLER, but without any remark about the contradiction with his own statement.

Further we find in the second part of the "Blüthendiagramme" in a well concealed corner, as a correction to the third footnote of p. 36 of the first part, the following sentence (17, II, p. IX): "wo convolutive Kronen vorkommen, da ist entweder die Deckungsrichtung überall absolut dieselbe, oder sie folgt dem kurzen Wege der Kelchspirale". EICHLER disregards here the exception mentioned before for *Statice* which he surely would have considered if he had been aware of the fact.

But as it was of much importance for the aim of the present paper to know the actual direction of the contortion, I have made a number of observations on different species of *Statice* and some allied genera; the outcome of these observations which I have treated in a separate paper (49) are indeed such as to confirm the conformity of *Statice* with other plants in this respect.

As remarked above, the progress of our knowledge after WICHURA is only scanty; the perusal of the literature after EICHLER often displays a sad state of confusion and ignorance.

In 1876 G. HENSLOW published a paper on the origin of floral aestivations (23) in which neither BRAUN, nor WYDLER nor WICHURA

were cited. The numerous observations recorded in this paper are of little value, as the mode of junction to the calyx is not duly taken account of, so that very different kinds of aestivation are put together and the discovery of the regularities of the conditions are impeded.

Moreover the whole view of the facts is not the right one. HENSLOW tries for instance to prove that the descendent corolla of the *Papilionaceae* as well as the ascendent corolla of the *Caesalpiniaceae* are quincuncial in origin, but that their proper form of aestivation is brought about by the fact that the fourth petal has come to overlap the second petal. One might ask how the same metatopy could give rise to two entirely different forms of aestivation : for HENSLOW the explanation is simply that in the *Caesalpiniaceae* petal number 1 is one of the two anterior petals, but in the *Papilionaceae* it is the posterior one, the vexillum. In this way the corolla spiral is the continuation of the calyx spiral only in the *Caesalpiniaceae*, not in the *Papilionaceae*.

The contort aestivation is to be derived according to HENSLOW from the quincuncial one, the cochlear aestivation being an intermediate step. This derivation is not confirmed by facts and must be taken as mere speculation.

Much more consistent is the attitude of SCHUMANN in his paper of 1886 (51) which is based entirely upon the developmental history. The principal distinction is that between the simultaneous and the successive development. The successive development gives rise to corollas with quincuncial, ascendent and descendent aestivation : in all these cases the aestivation is with very few exceptions the expression of the developmental order.

The simultaneous development on the other hand gives rise to corollas with contort, valvular or variably imbricate aestivation. In the last mentioned case the overlapping of the petals being all of the same age, is entirely due to chance.

SCHUMANN gives three instances from his numerous sets of observations : for *Primula elatior, Saxifraga crassifolia* and *Nonnea lutea*, of which he has observed 175, 194 and 72 flowers. He finds that the observed numbers of the different kinds of aestivation sufficiently correspond with a chance distribution.

Here too the position of the corolla with respect to the calyx is not mentioned, so that the observations cannot be adapted for a closer examination ; from his point of view this omission is however logically consistent.

The greatest difficulties are allied for SCHUMANN to the explanation of the contort corolla. Though he remarks that in cymose inflorescences the direction of the contortion often changes in consecutive flowers (51, p. 65), he does not know of the two kinds of contort aestivation of BRAUN. His developmental explanation is reduced to the supposition of a "rhytmische Ab- und Zunahme der Wachsthumsenergie in aliquoten Theilen des Blüthenbodens" (51, p. 67), a sentence that sounds very well, but

that cuts no ice; even if it should have been founded on observations one might say that of course the distribution of growth always must be such as to bring about the later form.

After a long pause a further paper is issued in 1927 by J. REINSCH (36), on the developmental origin of the aestivation. In contrast with SCHUMANN the mechanical factors are no longer considered as the most important ones, but it is now the symmetry of the flower, the "Gesamtsymmetrie", which determines the form of aestivation. For the contort corolla this symmetry is even called the cause (p. 113).

As symmetry does not belong to the natural forces, this should obviously not be taken to the very letter. But apart from this there are some valuable elements in the paper.

REINSCH finds that the ascendent and the descendent aestivation do not always correspond to the developmental order of the phyllomes, as SCHUMANN believed them to do, but that in many cases the characteristic overlapping is only a consequence of a later growth process; for *Verbascum* he even reports a complete change in the furthering of the sepals, so that the descendent developmental order finally leads to an ascendent aestivation of the calyx.

REINSCH rightly distinguishes between apical and lateral aestivation; the apical aestivation is found in the calyx to be of the same form as the lateral, in the corolla however he confirms without his knowledge the old result of BRONGNIART that the petals which at the outset are most furthered will become overlapped by the others later on.

In 1928 a paper by ZĀMELIS follows (69), on the strongly variable aestivation of *Pirola,* the same object studied by ROEPER more than three quarters of a century before. In this paper ZĀMELIS establishes two progressive series of aestivation forms, both starting from the quincuncial aestivation and leading the one to the changing, the other to the independent contortion. These series are however mere speculations, not based on facts and moreover not constructed in the right way. So for example the changing contortion is derived from the spiral arrangement in such a way that it would become contort after the long way of phyllotaxis. References to the older literature are lacking.

Much more satisfactory is the last paper I have to deal with here, that of H. J. LAM on the *Canarieae* (31). In this paper LAM reports on extensive observations on the aestivation of the trimerous corolla of one single specimen of *Canarium decumanum.* As there are only three petals, there are consequently only two kinds of aestivation, the $1/3$ spiral and the contort arrangement. Both occur in a right and a left form, so that altogether there are four modifications.

The aim of LAM was to determine whether SCHUMANN was right in assuming that the aestivation in plants with variable imbrication is only due to chance. Theoretically the four forms of aestivation are to be ex-

pected, if chance is the only governing factor, in the relation $3:3:1:1$, as LAM rightly points out.

On 3617 flowers of the same tree LAM indeed observes approximately this relation, yet with a rather constant deviation. He finds namely:

    r-spiral[1]) in 1584 flowers, or in every eight flowers 3.50
    l-spiral   1437 . . . . 3.18
    r-contort   344 . . . . 0.76
    l-contort   252 . . . . 0.56

We see that there are obvious deviations from the theoretical values; the spiral arrangements having too high, the contort too low values; these deviations are, as WELLENSIECK calculated on behalf of LAM, far beyond the error limits.

LAM adds: "Er wäre vielleicht zu fantastisch mit Beziehung zu einer phylogenetisch früheren Spiralstellung an ein atavistisches Element zu denken" (p. 33). Here I might propose a somewhat different view and pretend that the cause of the deviations is not of a phylogenetic kind, but ontogenetic. As we shall see farther on in many other plants, so here too the aestivation is only partly due to chance: at the moment in which the aestivation sets in, a moment which is also rather late during the development here, the differences in age of the three petals having not yet entirely been eliminated, their influence on the aestivation, though succinct, is still discernible.

There is hardly any doubt that the petal opposite sepal 3 will have had the highest percentage of overlapping edges, being the oldest petal in the spiral; unfortunately LAM does not indicate the position of his corollas in relation to their calyces.

There is still a second argument inducing LAM to a reserved attitude in regard to the spiral hypothesis, namely that the right spiral and the right contortion show a certain preponderance over the corresponding left arrangements: a difference which would remain unexplained in any case.

Such a difference is however not mysterious at all; there are analogous cases in literature. Thus BROOME found in PINUS LARICIO out of 1100 cones of a single tree 69.82 % l-spiral, which too is far beyond the error limit (communicated by CHURCH 15, p. 351). Such a condition may have different causes; it might for instance be explained by a preponderance of homodromy among the lateral branches of the specimen.

Summarizing this chapter we may say that the corolla aestivation is a phenomenon which arises only late during the development of the flower. When finally the petal edges meet, there may ensue an overlapping in a direction which is only subject to those small and inscrutable causes which we call chance, so that both directions occur in equal numbers.

In other plants there are peculiar causes giving a preponderance to a

---

[1])   For the definitions of r- and l-aestivation cf. Chapter 3.

certain overlapping, even sometimes to the extent that hardly any exceptions occur.

These causes may be connected with those for the zygomorphic development of the flower ; in such cases there arise more or less fixed relations between the aestivation and the position of the symmetry plane.

Further, the original difference of position and age of the petals in the spiral may still more or less determine the aestivation : in a few natural families to such an extent that the aestivation is throughout eutopic ; in other cases only a certain tendency to eutopy is left.

The contort corolla finally is considered by WICHURA on good arguments as a phenomenon quite analogous to that of twisted vegetative leaves. The causes of it remain entirely unexplained. In many plants the direction of the twist is fixed ; in many other plants the direction changes with the calyx spiral.

CHAPTER 3.

The different forms of imbricate aestivation and their nomenclature.

For the distinction of the different forms of imbricate aestivation [1]) it is of primary interest to determine the number of overlapping, half overlapped and quite overlapped phyllomes. As the pentamerous corolla is the most important for our purpose, I shall begin with the treatment of the pentamerous whorl.

In this whorl only two wholly overlapping phyllomes may be present, in which case there must be one half and two wholly overlapped ones. A simple deliberation shows us that this so-called quincuncial arrangement is possible in two antidromous mirror-images; considering the position of the corolla with respect to the calyx the number of permutations rises to ten. Only one of these ten is eutopic, the others are metatopic.

The two mirror-images may be distinguished as a right and a left spiral; it is only a question how to chose our definition. In my previous papers I have always followed in this respect the custom in use by the majority of botanists, i.e. I called a spiral a right-handed one, if it ascends to the right for an observer placed in its axis.

I knew very well that there was some confusion on this point, but as A. P. DE CANDOLLE, BRAUN, WYDLER, EICHLER and so many others adopted the same definition I felt perfectly easy on that score.

In 1931 however I was struck by the fine lecture of Prof. G. VAN ITERSON Jr., a presidential address to the Dutch Natural and Medical Congress at Delft, on the subject Left and Right in Living Nature (29). The arguments brought forward in favour of a definition in conformity with that used in other sciences were so strong, that I resolved to change my custom and to adopt the reverse definition.

In itself either definition is exactly of the same value. There would then have been only a reason for an individual botanical definition, in disregard of what other sciences might have chosen for their use, if there had been a biological meaning in either of the two. If the supposition of SCHIMPER that there should be a wave movement at the stem apex had been confirmed, or if GOEBEL's spirotrophy had been anything but a speculation, there

---

[1]) K. SCHUMANN (51) gives a set of formulae suited for the description of any individual case of imbricate aestivation of a whorl by means of certain symbols. This way of notation has later been much improved by R. WAGNER (58).

In the present paper these notations are not made use of as they are not only rather unsurveyable, but especially as they keep to the individual case and are not appropriate for the distinction of groups of cases belonging together as of common biological interest.

might have been a good argument for the usual botanical definition, as there would have been something creeping round the vegetative cone in an acropetal way, and therefore continually deviating from the tangent towards the right or left side. But as we have no reason to adopt such suppositions, we may just as well join with the other sciences and adopt their definition, which in Botany has been used already by LINNÉ, VON NÄGELI, WICHURA, SCHMUCKER, VAN ITERSON and others.

All ten permutations of the quincuncial aestivation occur in such plants where chance governs the aestivation; some of them may occur more or less constantly in zygomorphic flowers. When two lateral petals become overlapping, as IRMISCH described to be the case in *Rhinantheae* and some other groups, the consequence is a quincuncial aestivation which is metatopic and yet may be very constant. This form of aestivation which has not yet been distinguished by a proper name will be indicated in the present paper by the term c o n f l u e n t   a e s t i v a t i o n (Aestivatio confluens). This term has been chosen in analogy to the generally used terms ascendent and descendent to be treated below, which denote absolutely parallel phenomena.

In the second place we can have only one wholly overlapping phyllome; in that case there are three half overlapped and one wholly overlapped one. This aestivation has been called cochlear by all botanists since EICHLER, and I shall follow this practice. As EICHLER has already remarked (17, I, p. 7) and as our Fig. 3 may illustrate, the overlapped petal may lie next to the overlapping one, or it may be separated from it by one half-overlapping petal. The first form is called by HENSLOW imbricate proper, by CHURCH simply cochlear[1]). I shall call this form however v i c i n a l l y   c o c h l e a r, or by abbreviation v i c i n a l. The other form is called by HENSLOW half imbricate, by CHURCH bilateral; I shall call this one d i s t a l l y   c o c h l e a r or by abbreviation d i s t a l.

Both forms occur in two mirror-images and each of these in five different positions, so that there are 10 permutations of vicinal and 10 of distal

---

[1]) It is not my aim to discuss here the advantages and disadvantages of the different terms used through the course of time; those interested in that topic may be referred to the papers of ASA GRAY (22), HENSLOW (23), CHURCH (16) and REINSCH (36) in which they may find what they want.

The only point I wish to give a little information on is the name of a certain RICHARD which is a constantly recurring feature in the papers mentioned. The work of this RICHARD is never quoted, and his full name never given, the common source of information being a place in A. P. DE CANDOLLE (12, p. 521).

Having happened to come across a necrology of the year 1824 by CH. KUNTH (30) on LOUIS-CLAUDE-MARIE RICHARD, I succeeded in getting to hand the original work (10) which appeared to have been published in Paris and not in Amsterdam as KUNTH had written, the author's name being after the title page only *Louis-Claude Richard*. In this elementary volume we really find on p. 122 the article on "préfleuraison", mentioned in his biography, but only in the disappointing form of a short and utterly unimportant passage.

aestivation. The mirror-images will be distinguished in the present paper in the following way : when the overlapping petal as viewed from the outside of the flower lies on the right side of the overlapped one, the aestivation is called right-handed. Our Fig. 3, with the four principal cases, will make this better understood than words can do.

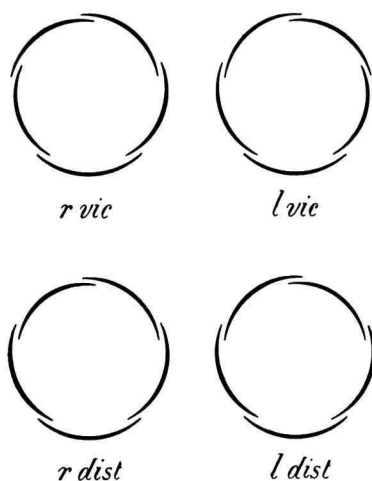*r vic*   *l vic*

r dist   *l dist*

Fig. 3. Diagrams of pentamerous whorls with vicinal and with distal aestivation in right and left configuration.

All these 20 cochlear aestivation forms may again be found in flowers with a variably imbricate corolla. But further there are here also some forms which may be found in a stable condition in zygomorphic flowers : we meet here namely with the forms which have been called by all botanists since WYDLER ascendent and descendent, being particular positions of distal aestivation. Amongst the vicinal aestivations stable forms are very rare : the only instance known to me is *Tropaeolum majus,* to be described in Chapter 6.

In the third place all petals may be half overlapping, an aestivation that has been called contort since the time of LINNÉ. Other terms are convolute and twisted ; I shall not use them, as the oldest one is quite serviceable.

Of this contort aestivation there are only two mirror-images, no permutations further being possible. Of these two I shall call right contort the one in which as seen from the outside every petal overlaps its right neighbour ; so I shall be in accord with LINNÉ, BRAUN, WYDLER and EICHLER, but in disaccord with WICHURA and SCHMUCKER [1]).

Further I shall call the independent contort aestivation of BRAUN a u t o t r o p i c a l l y c o n t o r t or by abbreviation a u t o t r o p i c and the changing contort aestivation h e t e r o t r o p i c a l l y c o n t o r t or by abbreviation h e t e r o t r o p i c. In the heterotropic aestivation we have as reported a fixed relation between calyx spiral and corolla contortion ; in our terminology a calyx with a right-hand spiral is followed by a right contort corolla, and reversely.

This form of heterotropy being indicated by EICHLER as "konvolutiv nach KW", after the short way of phyllotaxis, it will be designated in the present paper as heterotropic SW.

[1]) SCHMUCKER holds the opinion (41, p. 54) that the adoption of the definition of the right and left spiral as given by LINNÉ implies that the definitions of right and left contortion as used by nearly all botanists should be changed too. This however is a mistake ; the relation between the space spiral and the flat spiral is in the most literal sense of the word liable to be viewed from either side.

The other relation, that of the combination of a right spiral with left contortion which we shall meet with later on in the calyx of the *Cistaceae,* may be called then heterotropic LW.

In the autotropic contortion such a connection does not exist; for these cases, and for exceptional contort aestivations in plants with variably imbricate aestivation, we have to distinguish between the two possible connections and may do so in the analogous way by mentioning them as contort SW, being the same relation as that in SW heterotropy, and for the reverse condition in the same way contort LW.

Of course there may be still other forms of contortion in nature; we might for instance have plants where the same individual produced both right and left contort flowers, but without any relation to the calyx spiral, the direction of the contortion being determined by chance.

In the genus *Goniolimon* we shall meet with a case which is intermediate between heterotropic contortion and the form described here which would perhaps properly be called a n o m o t r o p i c.

Other forms of aestivation beyond the 10 quincuncial, the 20 cochlear and the 2 contort ones are not possible in the pentamerous corolla, as has been set forth already by CHURCH (16, p. 186) and LAM (31, p. 39). For whorls with a different number of members we may have similar distinctions which I will touch on here.

In dimerous whorls there are only four permutations in two types: two distichous forms of which one is eutopic, and two contort.

In trimerous whorls there are eight cases, namely six spiral of which one is eutopic, and two contort.

In tetramerous whorls the number of forms is 16; two decussate ones one of which is eutopic, eight vicinal, four distal and two contort.

In hexamerous whorls the number of permutations is 64; two forms with alternating trimerous whorls, one of which is eutopic, 30 where two members are wholly overlapping, two half- and two wholly overlapped, a category for which a name does not yet exist and neither is required for the moment; 30 cochlear, viz 12 vicinal, six distal and 12 "intermediate"; and finally two contort cases.

If necessary the distinction of ascendent, descendent and confluent may be carried out in the different cases.

CHAPTER 4.

Theoretical basis of research and methods to be followed.

§ 1. GENERAL CONSIDERATIONS.

In our first Chapter we saw that the curious mixture of spiral and whorled phyllotaxis in floral phyllomes has been interpreted by the first morphologists as due to the hypothetical fact that all floral whorls should be transformed spirals; wherever the transformation is not quite complete, traces of the original spiral are discernible.

This conception would indeed furnish a rational explanation of large numbers of facts which otherwise would give rise to the greatest difficulties. If really phyllotaxis is the outcome of the junction of younger phyllomes to the older ones, if in other words the HOFMEISTER's rule shall be the basis of our phyllotactical theories, a given arrangement may be either whorled or spiral, but not partly both at the same time, as I have remarked already before (44, p. 187).

It is only when we base our conceptions on symmetry tendencies, on phylogenetic processes of development or the like, and abandon the hope of an explanation with a causal back-ground, that both problems and difficulties vanish, as anything is now equally possible.

Now we might first ask why the general opinion is that whorls are to be derived from spirals and not reversely spirals from whorls which might perhaps equally meet our demands. There are indeed authors who have tried to solve the problems this way. I have already mentioned above how BRAUN had long been indetermined as to where the solution was to be sought, and for a long time tried to derive spirals from whorls; some years afterwards STEINHEIL published some papers (52, 53), which were very positive in the same direction, papers on which BRAUN wrote however that one should not waste one's time in contending with "dergleichen ohne alle Gründlichkeit und — was die Hauptsache ist — ohne geduldige, anhaltende und vorurteilsfreie Naturbetrachtung gemachte Sachen" (33, p. 282).

Another case is offered, by the derivation of the spiral arrangements in *Peperomia* from the decussation, by VON GOEBEL (20, confer too the paper by VON VEH, 56).

The deeper reason why as far as I see the majority of morphologists follows the reverse way is this, and it seems to me a quite convincing argument, that the spiral phyllotaxis is not only the prevailing one in Angiosperms, but that it is presented in most cases in a remarkably pure form, whereas whorls usually occur in a much less perfect form. For it is

not only in flowers that whorls show traces of a spiral origin, but in the vegetative region too they are often in the same condition, as the study of decussation fully proves (47).

The fact that all shoots in Dicotyledons begin with a more or less pure decussate phyllotaxis might be opposed as it seems to suggest the idea that this would be an original arrangement. In my opinion this does not hold true; the formation of false dimerous whorls which many Dicotyledons retain in the higher parts of their shoots is in my opinion the rule in their cotyledons and of common occurrence in their prophylls; the traces of the spiral in both cotyledons and prophylls may however often be recognized.

I hope to treat this point more extensively on another occasion, but am obliged to point out the principle here.

If we are inclined to regard any whorls in Angiosperms (in Pterido-phytes there may be other conditions) as transformed spirals, and therefore our Dicotyledonous corolla also, we may ask first which phenomena are to be expected for that case.

The best way to get an impression of what has to be expected may be gathered from a comparison of the corolla with the calyx, where the spiral is so much clearer. A survey of the phenomena to be observed in the calyx may therefore follow first.

One of the most prominent points is that the sepals usually have a successive origin; in pentamerous calyces in a quincuncial order. In tetramerous and hexamerous calyces the sepals are no more simultaneous in origin, but the succession is not so clearly spiral. According to PAYER (35), from whom all the present developmental statements are taken, the rule is that the "outer whorl" of two in a tetramerous calyx and of three in a hexamerous one arises before the "inner whorl"; the inner whorl is mostly simultaneous in origin, the outer whorl often successive, e.g. in *Menispermum, Rheum, Datisca*. These conditions correspond very well to similar phenomena in decussate foliage leaves.

The sepals ordinarily are about equidistant in the calyx whorl of actinomorphic flowers; it is only in some cases that BREINDL observed such differences as may be the outcome of the original spiral position (9).

In many pentamerous calyces the sepals, though arising in a quincuncial order, afterwards show a valvular or a reduplicate aestivation; in other cases they may become variably imbricate (*Grossularia*) or contort (*Phlox*). In those cases the original differences in ages are not sufficiently strong or not sufficiently preserved to withstand the disturbing action of other forces.

In some cases the sepals may arise simultaneously; this is only to be taken as a stronger action of the disturbing whorl forming factors. For the perigon of *Phytolacca* PAYER mentions a simultaneous origin, though later on the aestivation becomes quincuncial.

The zygomorphic flowers again present a different aspect. In certain cases the calyx, arising in a quincuncial order, keeps to the same form of

aestivation, though becoming decidedly zygomorphic; *Viola, Tropaeolum, Melianthus* and *Polygala* may serve as examples. Much more frequent are however the cases in which the developmental order is also changed, in accordance with the zygomorphy of the flower; thus we have an ascendent order of development in the *Trifolium* calyx, a descendent one in the *Labiatae* calyx and a confluent one in *Impatiens*.

All this points to the correctness of the view of EICHLER that the different development the parts of a zygomorphic flower are subject to, not only influences the later stages but also the very first primordial stages, so that even the order of arising is wholly changed; it is only a special case of the general rule that "Förderung" (which I shall translate by furthering, and "geförderte Organe" by furthered organs) causes an organ to become visible earlier than it would have done otherwise, and "Minderung" (translated here as repression, and "geminderte Organe" as repressed organs) retards the appearance.

It will be clear that for the corolla we have to be prepared to meet with analogous phenomena, but all shifted from the spiral side in the direction of the perfect false whorl, by the further completed metatopy.

In this respect we are not deceived. In a small number of cases we have the spiral origin and spiral aestivation of the corolla as clear as in so many calyces; these cases not only comprise such flowers where the flower is spiral throughout as in some *Ranunculaceae* or in *Nuphar luteum* (EICHLER 17, II, p. 182), but moreover flowers in which the corolla seems to be the last spiral belt, namely the *Ternstroemiaceae* and the *Hippocrateaceae*.

In most families the developmental order seems to be simultaneous, if not, by the action of the zygomorphy factors, the furthering or repression of some parts has changed the state of things.

A further fact, peculiar to the corolla, is the remarkable retardation of the final developmental stages. The aestivation consequently arises very late. This and the simultaneous origin, in consequence of the strong whorl-forming factors, make it clear that in determining the overlapping of the petals chance will have the greatest influence, unless zygomorphy factors or other special forces ensure the preponderance of a certain direction of overlapping.

In such cases therefore where remnants of eutopy may be preserved, we shall have to expect that these are only scanty, and only to be recognized by statistical treatment of a sufficient number of carefully executed observations.

To judge the value of any results in this direction we shall have to take recourse to the theory of probability, but even when we consult this doctrine to the full extent and in the right way, we must be aware of the fact that there may be several influences in the flower, like those of the zygomorphy factors, which may delude us by false results. Only a research

on a rather broad basis of facts may therefore possibly give satisfactory results.

Coming now to the methods to be used, it will be clear that these, though generally of a statistical nature, will be different for actinomorphic and for zygomorphic flowers. For the actinomorphic flowers we have moreover to distinguish between the variably imbricate and the contort aestivation. I shall treat these three successively in the following paragraphs.

§ 2. THE VARIABLY IMBRICATE COROLLA.

The first thing to be done of course is the observation of the aestivation in a number of flowers. For any corolla the peculiar form of aestivation is to be noted down, as well as the overlapping at each of the edges. This is done in the simplest way by numbering the petals; I always numbered them according to the supposed spiral with numbers following those of the calyx; in a pentamerous flower therefore as 6—10. The different edges may be denoted as 6—8 for the edge between 6 and 8; $^6/_8$ may represent the eutopic, $^8/_6$ the metatopic overlapping, and 6‖8 an open aestivation.

In this form the observations of a number of flowers may easily be written together in one single formula, and we may then proceed to the comparison with a chance distribution and to examine whether any conclusion from the figures may possibly be deduced.

In the first place we may compare the occurrence of the different kinds of aestivation with the chance values. For the pentamerous corolla we know that 32 different permutations may occur and it is not difficult to prove that each of them has the same $^1/_{32}$ chance. So we have a $^1/_{32}$ chance of getting a eutopic aestivation, $^9/_{32}$ for a metatopically quincuncial, $^5/_{16}$ for a distal, $^5/_{16}$ for a vicinal, and $^1/_{32}$ each for contort SW and contort LW.

But as we are dealing with limited series of observations, we have to expect that even where only chance distribution occurs, the observations generally will show deviations from the theoretical values. These deviations themselves are subject to the well-known law of normally fluctuating variability, and we may therefore only judge the value of a certain deviation by comparing it with the deviations which are to be expected.

We may do this by calculating a mean error or standard deviation (m or σ) or a probable error (r or Q or ε). For these values tables may be consulted (compare 43, p. 175).

The only disadvantage of this method is that the theory of probability as used here, does not consider the deviations as discontinuous. So amongst 25 flowers we may only find either 0 or 1 or more eutopic cases, but not 0.78125 as the theory would demand. The following table gives us therefore the nearest approach in whole numbers, with the probable error to one decimal place of the real value behind it.

As the probable error is the value half of the deviations will exceed, while the other half fall short of it, it is an easy basis for comparison with

Number of corollas	Cases of aestivation to be expected					
	eutopic	quincuncial	vicinal	distal	S W	L W
25	1 ± 0.6	7 ± 1.5	8 ± 1.6	8 ± 1.6	1 ± 0.6	1 ± 0.6
50	2 ± 0.8	14 ± 2.1	16 ± 2.2	16 ± 2.2	2 ± 0.8	2 ± 0.8
100	3 ± 1.2	28 ± 3.0	31 ± 3.1	31 ± 3.1	3 ± 1.2	3 ± 1.2
150	5 ± 1.4	42 ± 3.7	47 ± 3.8	47 ± 3.8	5 ± 1.4	5 ± 1.4

observed values. The more so as we know that in the case of a normal variability a deviation of 2r or more is to be expected once in 4.5 cases; of 3r or more once in 22.3 cases, of 4r or more in 142 cases, of 5r or more in 1341 cases, of 6r or more in 19.200 cases, of 7r or more in 330.000 cases.

For a more detailed analysis we must however compare the individual edges with the theoretical conditions; there it is obvious at once that a chance distribution will give in the long run 50 % of both possible kinds of overlapping. But we have to know more; when we find for example in a series of 25 flowers that at a given edge the one way of overlapping occurs 18 times, against the other only 7 times, what is our conclusion then to be?

When we take a series of 25 observations of a given edge as the unit, and we have a certain number of these units, the chance of getting a certain relation [1]) between the two possible kinds of aestivation, expressed as a percentage of the number of units and only to the first decimal place, according to the theory amounts to:

Relation between the two possibilities	Probability in %	Relation between the two possibilities	Probability in %
13 : 12	31.0	18 : 7	2.9
14 : 11	26.6	19 : 6	1.1
15 : 10	19.5	20 : 5	0.3
16 : 9	12.2	21 : 4	0.1
17 : 8	6.4		

[1]) The law is that for n observations of such a kind that only two results, a and b, are possible the chance to get n identical results a is $\frac{1}{2^n}$, the following terms for $n-1$ a and 1 b, for $n-2$ a and 2 b etc being $\frac{n}{2^n}$, $\frac{n(n-1)}{2 \cdot 2^n}$, $\frac{n(n-1)(n-2)}{3 \cdot 2 \cdot 2^n}$, which gives for the last term, the chance to get n identical results b, $\frac{n!}{n! \, 2^n}$ or $\frac{1}{2^n}$ like the first term. These terms represent the binomial coefficients of Newton.

The four following terms 22 : 3 up to 25 : 0 are less than 0.1 % and in practice are to be neglected ; the chance of finding 25 : 0 would accurately be 0.000 005 96... %.

We see thus that our instance of a relation 18 : 7 is a good indication, but no definite proof, of a real tendency to eutopic or metatopic aestivation, so that if possible we have to continue our observations.

For larger series of observations we may of course calculate similar tables, but as soon as the series is large enough we may also compare our results with the probable error as referred to above.

The application of the described method may sometimes meet with a peculiar difficulty, namely that the overlapping of two petals is different at the base and higher up ; sometimes there may be even two changes, the middle part being overlapped a different way from the base and apical part. At the places where the aestivation changes, the petals often are torn more or less into lobes.

In computing the number of deviations I used to note such cases as $\frac{1}{2}$ deviations.

§ 3.   THE ZYGOMORPHIC COROLLA.

In zygomorphic flowers we may observe in some plants a eutopic aestivation in the calyx ; beyond the examples cited above where moreover the quincuncial origin had been stated by PAYER, we may cite *Aconitum, Delphinium,* several *Malpighiaceae* and *Vochysiaceae.* This proves that zygomorphy and quincuncial arrangement may go very well together.

In the corolla however with its much weaker eutopy we may expect that the furthering or repression of the petals in a zygomorphic corolla may be much more dominating over any possible eutopy remnants, so that it is but natural that cases of eutopic aestivation in a zygomorphic corolla should be very rare or entirely wanting. The only case I ever heard of has been described by J. TROCHAIN (54, p. 840) for the *Malpighiacea Rhinopteryx.* Here too the possibility of the combination of eutopy and zygomorphy is fully established by this rare instance.

In most cases the zygomorphic corolla accordingly has an aestivation which is either ascendent, descendent or confluent in the symmetry plane [1]). We might ask whether under such circumstances there is still an opportunity left for further research. But here the illustrious example of the BRAVAIS brothers may lead us the way. We saw already in Chapter 1 that they had noticed in *Cercis* a difference in the ascendent aestivation of flowers with a left-hand and those with a right-hand spiral; I may

---

[1]) W. ROBIJNS distinguishes (37, p. 51) between the "plan de symétrie de la fleur" and the "plan de symétrie de la préfloraison". Usually the two coincide in zygomorphic flowers, but where the aestivation is variable they may have a different position.

The distinction is however not to be recommended as the aestivation symmetry plane in such cases has no biological sense.

refer the reader to our fig. 1. In our notation this amounts to a constant overlapping of petal 6 over petal 9 in the symmetry plane, a eutopic position.

From a theoretical point of view this remarkable fact may be explained in the following way. The zygomorphy factors act in such a way that the organs at both edges of the symmetry plane get different plastics. For organs situated on the right and left side of the plane, in corresponding places, the laws are quite similar, so that these organs will have the same plastics. For the two petals 6 and 9, lying on the anterior side of the flower on the right and left but at the same distance from the symmetry plane, the laws of differentiation are similar too, and there is no furthering or repression to be expected of the one as compared with the other. We may therefore expect that either by the general whorl formation the two will be wholly equalized and the aestivation will become a pure chance one, or we may expect that the original differences in age will more or less influence the aestivation; it is this last relation which has been recognized and clearly stated by the BRAVAIS.

But once so far, so many new questions arise, that I feel obliged to go somewhat deeper into the subject. The more as I have objected more than once in the previous chapters to the use of the symmetry principle as an explanation of the resulting form, a use which I have characterized as belonging to the domain of the "Naturphilosophie".

So I have now to point out how according to my views actinomorphy and zygomorphy may arise, and what kind of morphogenetic forces may be involved.

In all shoots we have a polar contrast between base and apex. This contrast is an expression of the general property of all living beings to form the different parts of their body in different ways, according to different laws.

Without this property all beings would be either amorphous or spherical, or perhaps have the form of raindrops and the like; by virtue of this property however they assume their endless varying shapes and are able to bring forth differently acting parts or organs. The means by which this differentiation is brought about are unknown, but we may imagine that in these different parts different factors or gens, or different combinations of them, become active which in other parts are inactive. In such a way locally different morphogenetic forces may be originated.

In the vegetative cone of the shoot the morphogenetic forces are remarkable for the fact that they cause a continuous formation of new organs, a strong growth and a never ceasing concentration of the most active forces in the centre, whilst the newly formed organs are elaborated and their growth finally is stopped.

The leaves on the vegetative cone are laid down according to the phyllotactical laws. By the new leaves local changes are brought about, introducing new morphogenetic forces. But the point of insertion of a

leaf originally did not differ from any other place on the stem surface.

When in most plants the stem and its leaves together form an actino-morphic construction, this is not due to a special law of symmetry, but simply to the absence of a peculiar differentiation. To produce similar parts is the more simple stage; for a differentiation, i.e. for the production of differently organized parts, the plant needs different plastic forces. This represents a higher stage of evolution.

A true whorled phyllotaxis, such as we may observe in many *Lycopods*, is no more symmetrical from a botanical point of view than the spiral phyllotaxis the same *Lycopod* shows in other parts of the same shoot. In both the leaves on the different sides of the stem are formed according to the same law; both constructions are actinomorphic.

Most botanists have always felt that this was the natural line of thought; it is only by the false application of mathematical or crystallographical conceptions, that some botanists like GOEBEL and CHURCH came to the erroneous view that only the apert, the valvular and the contort floral whorls really are to be considered as radially symmetrical. In Biology the use of mathematical notions is always risky, and crystallographical conceptions are to be applied fully only in such cases where the properties of the material are consequences of the existence of a space-lattice of similar particles, as may be the case in cell-walls, but not in cellular tissues.

In zygomorphic flowers, and in dorsiventral shoots in general, a second polar contrast is added to the existing one, namely a contrast between the morphogenetic forces at two opposed sides of the centre in the vegetative cone.

By this contrast two opposed sides of the shoot are formed according to different laws, and the organs placed on those sides receive different plastics. These sides may be the abaxial and the adaxial, or they may have another position.

About the cause of this difference we may make the following conjecture. On one side of the vegetative cone a peculiar morphogenetic factor or a complex of factors becomes active, or perhaps active factors become more or less inhibited. The whole complex of morphogenetic factors will thus be changed. The influence of this change will spread more or less to the left and the right, and will be felt least on the opposed side of the cone.

By the longitudinal growth the different parts will grow out into longitudinal strips.

Of course we may just as well suppose that it is not one side where a different factor becomes active, but that on two opposed sides the complex of factors changes; this supposition is however hardly different from the first one and as the whole guessing is very speculative, it is not worth while to enter into details.

The symmetry of the bodies originating in such a way necessarily must be of the same class as that of most animals: of the three theoretically distinguishable axes two are heteropolar, one homopolar. We therefore

come, beyond base and apex, to a dorsal and a ventral side and to a right and a left one; the way in which these names may be applied being of course arbitrary and requiring special definitions.

The right and the left sides must become each other's mirror-image, again not because of inner principles, but simply because the laws of the differentiation are the same, so that there is no reason for important differences, and the different position of the two sides with respect to the two heteropolar axes brings with it an inverse orientation of the analogous parts.

In such a way we do not yet get a real explanation of the origin of actinomorphic and zygomorphic organs; yet the way to such an explanation is shown, along a series of conceptions all being of a physiological nature.

According to these views it will be clear that a petal situated exactly in the symmetry plane, either at the dorsal or at the ventral side, must become bilaterally symmetrical in itself; all petals however which are placed more or less on the right or left side will develop in the domain of the radii with different morphogenetic forces, so that they will have a tendency to a skew development.

In the same way an edge between two petals will be subject to the influence of the zygomorphy factors at all sides, except only the position in the symmetry plane, either at the ventral or the dorsal side.

In the case of *Cercis*, observed by the BRAVAIS brothers, the mode of junction of the calyx, as found in the *Caesalpiniaceae*, is the cause of one of the five petals being placed exactly dorsally and one of the edges exactly ventrally and it is through this circumstance that they could get their result.

When we ask about the conditions in other zygomorphic flowers, we come upon the remarkable fact that this peculiar circumstance is not only to be found in *Cercis*, but that it is the general rule in zygomorphic flowers. When these flowers are pentamerous, it is the rule that in every whorl there is one unpaired organ which is situated in the symmetry plane, and one edge at the opposite side of the flower likewise in the symmetry plane.

For trimerous flowers and trimerous whorls the same holds true; tetramerous and hexamerous zygomorphic flowers which are rather rare have two phyllomes of every other whorl in the symmetry plane.

Exceptions to this rule are very rare; in *Tropaeolum* we have pentamerous whorls which follow the rule; the octomerous whorl of the stamens is also in a symmetrical position, but the trimerous carpel whorl shows a small but very constant deviation. And in the species of *Hibbertia* with transverse zygomorphy (EICHLER 17, II, p. 250) the pentamerous whorls do not follow the rule, but the carpel whorl on the contrary does.

But it is not only in zygomorphic flowers that such a rule prevails; in actinomorphic flowers we have the analogous rule that the members of all whorls usually are placed symmetrically in the median plane, in isomerous flowers as well as in the separate whorls of heteromerous flowers.

And even outside the flowers, we see that in dorsiventral shoots with distichous or decussate leaves the position of the symmetry plane shows a fixed relation to the position of the whorls, the common condition being that none of the orthostichies lies in the symmetry plane, but that they are to be found at equal distances from that plane at the right and left side of the stem, though there are cases in which two of the orthostichies fall in the median plane (*Thujopsis* and other zygomorphic *Cupressaceae*).

All these familiar facts, which may be matter of course for those who believe that the symmetry principle in itself is a morphogenetic force, become extraordinarily remarkable for those who earnestly try to explain the plant forms as much as possible on physiological lines. I cannot remember ever to have seen a mention of it in literature as a problem; yet the problem in my opinion is one of the first order.

Whether the explanation should be sought for in the direction of an adjustment of the leaf primordia to the symmetry plane or to the median plane, or inversely in the direction of an adjustment of the strips of the zygomorphy factors to the position of the leaf primordia may as yet be left out of consideration.

The fact that in pentamerous floral whorls one of the edges is nearly always situated exactly in the symmetry plane is however beyond doubt, and is of primary interest for our topic. For in such edges the zygomorphy factors being at equilibrium are not likely to affect the aestivation, and it is in such edges that remnants of eutopy are to be sought for in the first place, of course by the statistical method.

The other edges theoretically might perhaps also offer an opportunity; we might look for deviations from the prevailing zygomorphic aestivation and determine statistically whether they were more numerous in such edges where the zygomorphic aestivation is a metatopic one than in such edges where the zygomorphic aestivation at the same time is eutopic; as however the deviations from the zygomorphic aestivations are rare, this is not a promising line of research and I have not followed it as yet.

§ 4.   THE CONTORT COROLLA.

The task of investigating the contort corolla as to its secrets, at first seems to be a rather hopeless one; the uniform way in which all margins overlap is not such as to give a starting point for any research.

It will however be clear that if anything, the important distinction between the autotropic, the heterotropic, and perhaps the anomotropic form should be able to furnish a key for the understanding of the phenomena; further the parallel drawn by WICHURA between the contortion and the twist of foliage and other leaves has to be duly considered.

The best plan to get some insight into the problem is of course to review the facts as known at present. I shall therefore give a survey, and shall do this separately for the two principal forms.

A. The autotropic corolla.

In the plants with autotropic corollas it is obvious that the calyx spiral is different in the different flowers here as well as in plants with heterotropic corollas. Yet the petals always overlap towards the same side. The petals may therefore be insensible to a stimulus which determines the direction of contortion in the heterotropic corolla, or perhaps the stimulus itself may be wanting.

The side towards which the petals overlap is often constant for whole genera or even families. From WYDLER (62), WICHURA (60) and especially from EICHLER (17) we may gather the following list, in which for comparison the Monocotyledons have been inserted too.

The right-hand contort are: *Liliaceae*: *Paris*; *Iridaceae*: *Iris, Tigridia*; *Bromeliaceae*; *Convolvulaceae*; *Polemoniaceae*, with deviations; *Hydrophyllaceae*: *Ellisia*; *Asperifoliaceae*: *Myosotis*, with deviations; *Cordiaceae*; *Solanaceae*: *Datura*; *Oleaceae*: *Chionanthus virginica*; *Jasminaceae*: *Nyctanthes, Jasminum officinale*; *Gentianaceae*: the majority; *Loganiaceae*: *Fagraea, Potalia*; *Apocynaceae*: about half of the genera; *Asclepiadaceae*: the majority of the genera; *Rubiaceae*: *Exostemma*; *Primulaceae*: *Anagallis, Trientalis*, many *Lysimachieae, Lubinia, Cyclamen, Samolus*; *Ebenaceae*; *Plumbaginaceae*: *Armeria*; *Epacridaceae*: *Epacris*; *Ericaceae*: *Erica*; *Papaveraceae*: *Meconopsis*; *Caryophyllaceae*: *Diantheae*; *Limnanthaceae*; *Crassulaceae*: *Bryophyllum, Kalanchoe*; *Saxifragaceae*: *Philadelphus hirsutus*; *Onagraceae*; *Haloragidaceae*: *Haloragis*; *Combretaceae*: *Quisqualis, Combretum purpureum*; *Melastomaceae*.

The left-hand contort are: *Hydrophyllaceae*: *Nemophila*; *Acanthaceae*: many genera; *Jasminaceae*: *Jasminum hirsutum*; *Loganiaceae*: *Geniostoma*; *Apocynaceae*: about half of the genera; *Asclepiadaceae*: the minority of the genera; *Rubiaceae*: *Pavetta, Ixora, Wendlandia, Augusta, Randia, Gardenia*; *Myrsinaceae*: *Ardisia*; *Sapotaceae*: *Isonandra*; *Papaveraceae*: *Glaucium*; *Droseraceae*: *Drosera* mostly; *Saxifragaceae*: *Philadelphus coronarius*; *Turneraceae*: mostly.

We see that the phenomenon occurs in a great number of families which are lying so far from each other in the natural system, that we may safely conclude it is of a polyphyletic origin.

Perhaps the contortion has some biological advantage in promoting an even and undisturbed development of the petals in the bud by the even space-filling; perhaps the advantage may be in an easier opening of the bud or something like that.

In the second place we have to pay attention to the fact that the list also includes plants with a zygomorphic corolla; among the contort *Acanthaceae* several are clearly zygomorphic (WYDLER 62, p. 124, EICHLER 17, I, p. 218); in other zygomorphic *Acanthaceae* we have an ascendent aestivation (*Stenandrium, Aphelandra*) or a confluent (*Adhatoda*). The two tendencies, that to contortion and that to zygomorphy

are both present, and the resulting aestivation may be more influenced by the one or by the other.

In the third place we may learn from our list that the right contortion is much more frequent than the left. This fact has already been fully recognized by WICHURA in 1852 (60, p. 70) and has been brought into line with the fact that the general trend of torsion in other kinds of phyllomes runs in the same direction, a fact also remarked first by WICHURA.

WICHURA says that when a leaf is twisted to different sides in different stages of its development, it is always a change from a right spiral into a left one. And when a leaf shows at the same time two different torsions, one in its apical and one in its basal part, it is always the older part, the apex, which is twisted to the right (in WICHURA's reversed terminology to the left) and the younger part, the base, to the left: the only exception to this rule known to him being *Alstroemeria peregrina*, which shows the reverse condition.

He continues then: "Eine Anwendung desselben Gesetzes lässt sich nun aber auch bei den nur nach einer Richtung gewundenen Blättern nachweisen, insofern sie entweder gänzlich, oder was den gewundenen Theil betrifft, als Metamorphosen der Spitze oder der Basis des Blattes anzusehen sind. Die Spitzen der Blätter, also z.B. die Griffel, Narben, Antheren und vor allem die Blüthenblätter in der aestivatio contorta, die zu einer Zeit winden, wo erst die Spitze des Blattes aus dem Blüthenboden sich hervorgehoben hat, verfolgen in überwiegender Mehrzahl die Richtung nach Links"[1]).

Now it is clear that when we take WICHURA's puzzling result for granted, that the leaves of Angiosperms have a tendency to become twisted to the right at their apex and to the left at their base, and when with him we compare the young petals with leaf apices, the direction of the autotropic corolla must be right contort in the majority of cases, or as WICHURA calls it: "nach Links gewunden".

"Auch die Spreite der Laubblätter ist als eine obere Bildung noch vorherrschend, wenn gleich nicht in demselben Grade häufig, links gewunden" follows on the above cited passage and from his systematic enumeration we may gather that he observed right twisted leaves in 32 species of Dicotyledons against left twisted in only 17; this result surely deserves our attention and should if possible be checked.

Of course this reduction to a particular case of a more general rule is not yet an explanation of the mechanism by which the necessary obliquity of the insertion of the petals is brought about. Yet we may gather from it that a general tendency to obliquity may be the starting point for the origin of the contortion.

------- --- ---

[1]) In view of the excellent observations and their abundant wealth, it is the more a pity that GOEBEL in his "Entfaltungsbewegungen" (21) has overlooked this predecessor.

A further remarkable fact, though not to be read from our list, is that the individual petals of contort corollas often are unequal-sided, becoming thereby skew, if not in position, yet in shape.

This has been described first by A. DE ST. HILAIRE and WYDLER for some heterotropic corollas, but has been confirmed by SCHUMANN for some autotropic too (51). SCHUMANN went too far in assuming that the lopsidedness was of universal occurrence in all contort corollas; REINSCH saw perfectly symmetrical petals in the autotropic *Datura* and *Exacum* (36, p. 113); I myself in *Phlox paniculata* and *Armeria maritima*.

In our chapter 2 it has been mentioned how SCHUMANN tried in vain to explain the contortion from growth processes. In his explanation the unequal-sidedness plays an important rôle, but his obscure reasonings only give the impression that the subject is not clear to himself either.

The natural view in my opinion is to take this lopsidedness as one of the possible consequences of the contort condition, not as one of its causes.

Passing from these general considerations to the question of how to frame a research method, we soon recognize that in perfectly contort corollas it is impossible to get a starting point for any research. There are however many plants in which the contortion is less perfect, in which deviations occur; these deviations may become numerous even to such an extent, that the aestivation practically changes into variably imbricate. In plants with a sufficient number of such deviations we may determine statistically whether the number of returns to eutopy is relatively greater than the number of deviations from eutopy to metatopy.

In practice this amounts to the following. When we have a pentamerous flower and a right contort corolla, a flower with a right-hand calyx spiral must be contort SW and must reach this condition by the metatopic overlappings $8/6$, $9/7$ and $10/8$, the two other edges keeping the eutopic overlappings $6/9$ and $7/10$. In a flower with a left-hand spiral which must be contort LW it is exactly the reverse, the metatopic overlappings $9/6$ and $10/7$ being required only, while the three other edges must remain eutopic.

We have therefore to record the deviations of a certain number of flowers with a right-hand spiral and of a certain number of left-hand flowers, and compare the results in the proper way.

If we find the metatopic and eutopic overlappings in about equal numbers, nothing is to be concluded; when on the other hand the eutopic overlappings clearly prevail, this may be due to the influence of the original spiral.

B. The heterotropic corolla. The salient point here is not only the alternation of the direction of the contortion, but perhaps still more the constancy of the SW heterotropy, of the relation between calyx spiral and contortion direction, namely that a flower with a right calyx spiral has a right contort corolla, and reversely.

The phenomenon of the heterotropic corolla is somewhat less widely

distributed than that of the autotropic; the following survey which is parallel to that of the autotropic corolla will prove that.

Plumbaginaceae: *Statice*; *Epacridaceae*: *Lysinema*; *Caryophyllaceae*: *Lychnideae* (some of which cochlear); *Cistaceae*; *Tamariscineae* (sometimes cochlear); *Ternstroemiaceae*: *Bonnetieae*; *Clusiaceae*: *Renggeria, Platonia, Maronobea*; *Ochnaceae*: *Sauvagesieae*; *Dipterocarpaceae*; *Sterculiaceae* mostly; *Malvaceae*; *Geraniaceae* with many exceptions; *Oxalidaceae*; *Linaceae*: *Linum, Reinwardtia*; *Trigoniaceae*; *Papayaceae* with exceptions, *Euphorbiacae*: *Ricinocarpus*; *Rosaceae*: *Gillenia*.

Notwithstanding the list is much shorter than that for the autotropic corolla, it gives a strong impression of a polyphyletic origin of the phenomenon by the diversity of the plant types.

The family of the *Trigoniaceae* with their strongly zygomorphic corollas, reminding one of that of the Papilionaceous flower, gives a remarkably close parallel to the autotropic and zygomorphic *Acanthaceae* and clearly proves that the contortion is not a consequence of a special kind of symmetry axis, a C_5 according to a crystallographical notation.

In our Chapter I we saw that some authors took the valvate and contort aestivation as the expression of the radial symmetry of the axis. REINSCH even wrote (36, p. 113): "Niemals findet sich eine derartige Ästivation bei dorsiventralen Blumenkronen". A statement that is surely contradicted by the facts.

The case is in some respects parallel to that of the valvate calyx of the *Columniferae*, mentioned already before, which is clearly quincuncial in origin, which determines by its spiral the contortion direction of the corolla and which is yet perfectly valvate. These conditions should be incompatible according to the view of GOEBEL and CHURCH that the valvate aestivation is the expression of a radial symmetry.

When we compare our list of plants with heterotropic corollas with that of the autotropic corollas we see that in most families we meet with only one of the two, either the one or the other. Yet three instances of both kinds of contortion occurring in a single family are to be found, in the *Plumbaginaceae*, *Epacridaceae* and *Caryophyllaceae*.

This coincidence tends already to raise a presumption that the two phenomena may be of a kindred nature. This belief is much strengthened by the following facts.

In the *Plumbaginaceae* we have not only both forms of contortion and even indications of a third form, the anomotropic one, but moreover we may have transitions between them. In my paper on the inflorescence of the *Plumbaginaceae* (49) I described an instance of a transitional form between heterotropy and anomotropy, in *Goniolimon tataricum*; from a statement by EICHLER we may infer on a transition between autotropy and anomotropy in a *Plumbago* (cf. 49) and a transition between auto- and heterotropy has been described by WICHURA for *Acantholimon Hohenackeri*. WICHURA writes about *Statice* (60, p. 90) that: "in deren zwei-

reihigen Blüthenständen rechts- und linksgewundene Knospen regelmässig mit einander abwechseln. Es scheint jedoch dieses Gesetz nur bei den blaublühenden Arten der Gattung *Statice* rein zum Vorschein zu kommen. Zwei roth blühende Arten, worunter *St. acicularis*" (after the Index Kewensis a synonym of *Acantholimon Hohenackeri*) "zeigten dagegen vorherrschend rechtsgewundene Blüthenknospen mit Beimischung einer geringen Anzahl links gewundener."

A second fact pointing in the same direction is that the petals of the heterotropic corollas show the same symmetry as those of the autotropic ones: they are in some species perfectly symmetrical, in other species lopsided, and in the latter case it is always the overlapped side which is furthered.

Asymmetrical petals are recorded by A. DE ST. HILAIRE for *Sida*, (24, p. 387), by WYDLER for *Malva* and *Hibiscus* (67, p. 359, by SCHUMANN for *Kielmeyera* and *Dombeya* (51, p. 66) and I myself may add *Linum austriacum, Oxalis floribunda, O. Ortgiesii* and *Plumbago Capensis.*

On the other hand I observed perfectly symmetrical petals in *Linum usitatissimum, L. flavum, Gypsophila paniculata, Geranium sanguineum* and *Plumbago Larpentae.*

In one and the same genus (*Linum, Plumbago*) we may therefore meet with both forms of petals. The conclusion is obvious that the unequal-sidedness may be brought about by conditions prevailing in the bud.

If now the autotropic and the heterotropic contortion are nearly related phenomena, it remains the more puzzling how the direction of the SW heterotropic contortion may be brought about. In our second chapter we saw that BRAUN had stated that the relation of the calyx spiral and the contortion direction was always the same, in all families. This statement has never been refuted, but for the fact that EICHLER did once describe a LW heterotropy for the genus *Statice*. And as I mentioned this had led me to my investigation on the corolla aestivation of the *Plumbaginacae* (49), a study which indeed confirmed the validity of BRAUN's general rule for *Statice* too, the heterotropy being SW and not LW.

In my preliminary communication on the contort corolla (46) I have already given an hypothesis for explaining the cause of this remarkable rule; it needs to be repeated here.

If we compare a flower with a left-hand calyx spiral and left contort corolla (Fig. 4A) with a flower with left-hand calyx spiral and eutopic corolla (Fig. 4B) we see that the difference is brought about by a different overlapping of the petals at three edges: 6—8, 7—9 and 8—10, marked in Fig. 4B by asterisks.

If therefore the heterotropic corolla is originated by metatopy from a spiral arrangement, the change is not brought about in the most simple way. If there had occurred two metatopies namely $9/6$ and $10/7$, the result would have been contort as well, but contort LW, not SW.

Now I believe that we may conceive why this apparently shorter and

easier way is not followed in nature. If namely the petals, though arising simultaneously to the eye, have really been laid down in a spiral order, petal 6 must be the oldest amongst them.
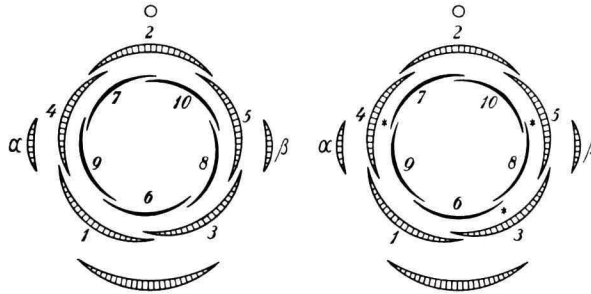

Fig. 4.   Diagrams of pentamerous perianths with heterotropic corolla (A) and with eutopic corolla (B). From (46), fig. 1 and 2.

If this petal has a tendency to a slight twist, but the direction of the twist has not been fixed beforehand as in the case of the autotropic corolla, it is reasonable to suppose that the surroundings may furnish the stimulus for the determination of this direction. In these surroundings we hardly find anything but sepal 1 and 3; and the idea is at once conceived that indeed the junction to 1 and 3 with their different insertion levels may be the determining factor.

The next petals, 7 and 8, will then be induced to the same skewness by their junction to the sepals 2 and 4 and to 3 and 5.

For 9 and 10 the junction to the sepals in itself would give a skewness towards the reverse side; if this should occur no contortion would ensue at all. It is however very probable that the petals 9 and 10 are carried along by the three older ones, 9 by the margins of 6 and 7, 10 by those of 7 and 8.

Of course I must grant that the whole conception is hypothetical. Yet the advantages reached in this way are rather considerable. It is the first trial made in literature to explain the fixed relation between calyx spiral and contortion direction, and it does not make use of any mystic "natur-philosophisches" principle; it only starts from the general fact of skewness in many phyllomes and from some simple suppositions which may be described in terms of matter and force.

Further it renders justice to the natural relation between the different kinds of contortion and to the existence of transitional forms of them; it leaves full room for the existence of zygomorphic contort corollas as well as for transitions between contortion and variable imbrication.

Moreover we shall see that in the course of our research a certain amount of facts will be described which tend to make the hypothesis still more a probable one. We may however try to check it also by comparing the heterotropic corolla contortion with similar phenomena in other vegetable

parts, and perhaps in the examination of these the rule that identical causes produce identical results may be of some use.

As far as I know for such a comparison there are three groups of facts which ought to be considered: the heterotropic calyx aestivation in the family of *Cistaceae*, the alternating contortion of foliage leaf pairs in many decussate plants, and the contortion of the cyathia appendages in many *Euphorbia* spp.

The heterotropic contort aestivation of the *Cistaceae* calyx only pertains to the sepals 3, 4 and 5; sepal 1 and 2 which may have their own different plastics and which then usually are much smaller than the inner sepals, are wholly overlapping.

The direction of the contortion depends upon the calyx spiral as in the heterotropic corolla; there is however one great and important difference: it is namely not an SW contortion, but an LW one.

And as the corolla in this family usually is also heterotropic, the calyx and corolla of every individual flower are antidromous in their contortion, as our Fig. 5, a reproduction of EICHLER's diagram of *Helianthemum vulgare*, will make sufficiently clear.
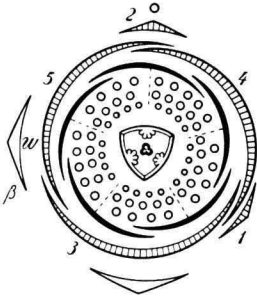

Fig. 5. *Helianthemum vulgare*. From EICHLER (17, II, p. 230, fig. 90 B).

The question of course arises whether this curious contrast may show some light on our problems; whether it may serve to invalidate or to corroborate the above hypothesis. A closer consideration soon reveals that the explanation of the contrast does not present serious difficulties and that it even tends to corroborate our views.

When petal 6, between sep. 1 and 3, becomes skew according to our conception by the combined influence of these two sepals or rather by their insertion at different levels, this is a kind of junction according to a ternary and a quinary parastichy; a junction which is not identical with the junction of the newly formed leaves, as it occurs much later, but which is analogous in every respect.

For the calyx such a junction necessarily has to bear a different character than for the corolla. The petals forming a false whorl are placed over another false whorl, the calyx. Underneath the calyx there is however no false whorl but there are either foliage leaves, in terminal flowers, or prophylls, in lateral ones.

Now it is clear that false whorls will join to each other in a peculiar way; their tendency to alternation makes this especially clear. It is therefore not a strained supposition that sep. 3 will join to sep. 1 and to β or the highest foliage leaf; indeed for any other supposition there is hardly room. In the same way sep. 4 will join to 2 and 1, and sep. 5 to 3 and 2: in other words the junction will occur after a binary and a ternary parastichy, whereas petals 6, 7 and 8 join to the calyx after a ternary and a quinary.

Such a junction however necessarily will give the reverse skewness and

thus cause an LW contortion. The fact, that the heterotropic corolla contortion is SW in all plant families, the calyx contortion LW in the only family in which it is known, may therefore be quite conceivable, and the hypothesis of the origin of the heterotropic corolla aestivation decidedly gains in probability by it.

As a second group of facts which may be of interest in this connection I mentioned above the contortion of foliage leaves to be observed in many decussate plants. The common condition here is that when contortion occurs, the successive leaf pairs of one and the same shoot are alternately SW and LW contort.

A review of the facts from literature and the examination of some natural objects brought me to the conviction that this phenomenon only shows a superficial likeness to the corolla heterotropy and that it is to be taken as a response of the plant to certain conditions of space-filling in the bud. As this however forms a subject of its own, I may refer the reader to the note soon to be published about it (50).

In the third place I mentioned the contortion of the cyathium appendages of a number of *Euphorbia* species.

The curious parallel between these appendages and petals has been fully treated of late by TROLL (55); from his description we might gather that in *Euphorbia fulgens* the appendages are usually right contort, and that left contort cases sometimes occur.

A direct investigation of the same species taught me however that the appendages are without any doubt SW heterotropic contort, in the terminal cyathia of the lateral inflorescences as well as in those of the cincinni; in the latter they are consequently alternately right and left contort.

A detailed description of these facts may follow in a separate paper, but here we have to face the fact of the SW heterotropic aestivation and to use it as a test for the above hypothesis about the origin of the heterotropic corolla.

The old and well-established conception that the involucral bracts subtend the cincinni of male flowers and that the glands and appendages are nothing but secondary commissural formations is in full harmony with the developmental facts: the involucral bracts arising first, in a quincuncial order continuing the phyllotaxis of the lower phyllomes, and the glands and appendages being formed later on.

When we now suppose that the appendages of *Euphorbia fulgens* and related species have the same undetermined tendency to skewness as the petals in plants with heterotropic corolla aestivation, it is not difficult to understand how an SW heterotropy may be induced here.

The first appendage to arise, and therefore the first to reach the susceptible stage, will be the one situated between involucral bract 1 and 3, indicated in our figure 6 as *a*. This appendage which is developed in close contact with the involucral bracts 1 and 3, necessarily gets in this way the required skewness direction. One might also think of an influence

of the two bracts a and γ which would give the same skewness; but these have not only a much more remote position, but moreover the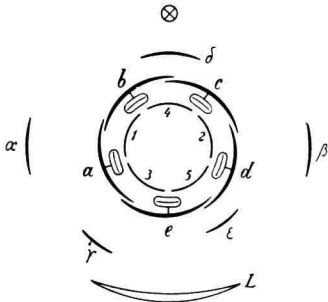y often fail, as many cyathium pedicels with the same contortion have only two bracts, corresponding to δ and ε of Fig. 6.

The next appendix in age will probably not be that one between 2 and 4, as was the case with the petals, but rather that between 1 and 4, indicated as b. Our fig. 6 will make it clear that the developmental order of the involucral bracts may be as indicated by the letters a—e, successively between 3 and 1, 1 and 4, 4 and 2, 2 and 5, and 5 and 3.

The only thing to be assumed further on this basis is that the direction of the skewness of b is not determined by the inner contact with 1 and 4 or by the outer contact with a and δ, but by a; 1 and 4 or a and δ would give the reverse skewness so that no contortion would be possible. The rest then follows without any difficulty.

Fig. 6. *Euphorbia fulgens.* Diagram of bracts and involucre of main axis of lateral inflorescence. L subtending foliage leaf; a — ε bracts, 1 — 5 involucre, a — e petaloid appendices.

Of course this conception is hypothetical like the former ones; yet it is not only clear that in this or a similar way an explanation of the appendages contortion may be reached, but that moreover the explanation of the heterotropic corolla aestivation is corroborated by the fact that the same supposition of an indeterminate skewness direction may be able to explain the different cases of this kind in Dicotyledons.

Returning after these long digressions to our proper subject, the heterotropic corolla and how to frame a method for its investigation, it will be clear that such a method has to be based, as in the case of the autotropic corolla, on the presence of deviations from contortions, i.e. on faults. In our pentamerous corollas these faults must be the eutopic positions $6/8$, $7/9$ and $8/10$, or the metatopies $9/6$ and $10/7$; and we may determine the frequencies of these different faults in a given plant.

Of course the faults may be distributed at random, so that the rate of the different frequencies is about the same.

If however in any plant the influence of the original spiral arrangement is still preserved at the moment in which the aestivation sets in, the eutopic faults or the rational faults as I have called them may be of a higher frequency than the metatopic or irrational faults; when we therefore find frequencies of the rational faults which evidently surpass those of the irrational faults, we may conclude that it is due to the influence of the spiral origin.

CHAPTER 5.

Observations on plants with variably imbricate corolla aestivation.

The plants usually indicated in literature as having a variably imbricate corolla may still show a number of differences in that aestivation.

I shall treat them accordingly in four different paragraphs and shall add a fifth paragraph for a discussion of the results.

All flowers were observed sub anthesi when it was quite sure that the aestivation was still the same as that one originated in the bud; as soon as this became uncertain they were observed in the expanding or even in the bud stage.

§ 1. Plants with an evenly distributed tendency to eutopic aestivation.

1. *Ranunculus Lingua.* Observed 25 flowers. Cases of aestivation: 1 eutopic, 5 metatopically quincuncial, 9 vicinal, 6 distal, 4 mixed, i.e. with one or more edges open or different at different levels. Metatopies: $6^1/_2$ cases of $^8/_6$, $10^1/_2$ of $^9/_7$, $6^1/_2$ of $^{10}/_8$, $9^1/_2$ of $^9/_6$, $6^1/_2$ of $^{10}/_7$. Together $37^5/_2$ metatopic against $83^5/_2$ eutopic overlappings.

Conclusion. The observed forms of aestivation when judged by themselves might have been due to a chance distribution; the five edges however show a marked preponderance of eutopy which is, as judged from the limited number of observations, distributed evenly over the edges.

2. *Hibbertia volubilis.* Observed 10 flowers. Cases of aestivation: 1 eutopic, 3 metatopically quincuncial, 3 distal, 3 mixed. Metatopies: 3 cases of $^8/_6$, $6^1/_2$ of $^9/_7$, $2^1/_2$ of $^{10}/_8$, $2^1/_2$ of $^9/_6$, 1 of $^{10}/_7$. Together $14^3/_2$ metatopic against $33^3/_2$ eutopic overlappings.

Conclusion. As far as can be judged from the few observations, a marked preponderance of eutopy, perhaps evenly distributed over the edges.

3. *Dryas octopetala.* Observed 25 octomerous flowers; those with 7 or 9 sepals having been discarded. Cases of aestivation: 8 with three petals wholly outside, 14 with two, 2 with one and 1 flower partly open. Metatopies: 7 cases of $^{12}/_9$, 8 of $^{13}/_{10}$, 12 of $^{14}/_{11}$, 11 of $^{15}/_{12}$, 13 of $^{16}/_{13}$, 4 of $^{14}/_9$, $7^1/_2$ of $^{15}/_{10}$, 13 of $^{16}/_{11}$. Together $75^1/_2$ metatopic against $124^1/_2$ eutopic overlappings.

Conclusion. Undeniable tendency to eutopy which may be evenly distributed, though the number of observations should be much extended to prove this with certainty. It is remarkable that the three petals 9—11

which ought to be wholly overlapping have respectively 11, $15^1/_2$ and 25 metatopies. Whether the increase is accidental or not, remains uncertain.

§ 2. PLANTS WITH A MARKED TENDENCY TO EUTOPY WHICH IS HOWEVER WEAKENED OR ALTOGETHER ABSENT AT ONE OR MORE EDGES.

4. *Passiflora coerulea.* Observed 50 flowers. Cases of aestivation: 22 eutopic, 15 metatopically quincuncial, 5 vicinal, 8 distal. Metatopies separately counted for flowers 1—25 and 26—50: 1 and 0 cases of $^8/_6$, 8 and 6 for $^9/_7$, 12 and 12 for $^{10}/_8$, 4 and 6 for $^9/_6$, 1 and 2 for $^{10}/_7$. Together 52 metatopic against 198 eutopic overlappings.

Conclusion. The observed forms of aestivation have already made clear that there must be a strong tendency to eutopy. Four of the five edges confirm this in different degrees, 6—8 and 7—10 being nearly always eutopic. At the edge 8—10 the tendency however is not to be observed.

Remark. The frequent occurrence of the metatopy $^{10}/_8$ has already been observed by AL. BRAUN, who took this as a proof of a reversal of the spiral direction between calyx and corolla: "Es lässt sich ... denken, dass im nächsten Wirtel der Umlauf der Blattstellung entweder dieselbe Wendung zeigt wie im vorausgehenden, oder die umgekehrte. Beide Fälle kommen wirklich vor. So sieht man z.B. bei *Passiflora coerulea*, bei welcher die Aestivation wohl schwerlich trügt, die Blattstellung in der Blume der umgekehrten Richtung folgen als im Kelch (Taf. 32, Fig. 3), während bei den Rosen und Ranunkeln die Stellung durch Kelch und Blume in derselben Richtung fortschreitet" (1, p. 363).

5. *Candollea cuneiformis.* Observed 50 flowers. Cases of aestivation: 14 eutopic, 15 metatopically quincuncial, 10 vicinal, 9 distal, 1 SW, 1 LW. Metatopies, separately counted for flowers 1—25 and 26—50: 0 and 3 cases of $^8/_6$, 5 and 10 of $^9/_7$, $16^1/_2$ and 10 of $^{10}/_8$, 2 and 3 of $^9/_6$, 2 and 3 of $^{10}/_7$. Together $54^1/_2$ metatopic against $195^1/_2$ eutopic overlappings.

Conclusion. The conditions are remarkably like those of *Passiflora*. The strong tendency to eutopy is already evident from the observed forms of aestivation; the five edges confirm this but for the edge 8—10, where no tendency to eutopy is to be observed.

6. *Rosa canina.* Observed 25 flowers. Cases of aestivation: 3 eutopic, 9 metatopically quincuncial, 5 vicinal, 6 distal, 1 SW, 1 partly open. Metatopies: 6 cases of $^8/_6$, 8 of $^9/_7$, $12^1/_2$ of $^{10}/_8$, 4 of $^9/_6$, 8 of $^{10}/_7$. Together $38^1/_2$ metatopic against $86^1/_2$ eutopic overlappings.

Conclusion. A weaker, yet still undeniable tendency to eutopy; only at the edge 8—10 is it not to be observed.

§ 3. PLANTS WITH AN EVENLY DISTRIBUTED CHANCE AESTIVATION.

7. *Ranunculus acris.* Observed 50 flowers, 25 in 1931, 25 in 1933. Cases of aestivation: 3 eutopic, 13 metatopically quincuncial, 15 vicinal, 10 distal, 3 SW, 2 LW, 4 mixed. Metatopies, separately counted for

flowers 1—25 and 26—50: 14 and $9^{1}/_{2}$ cases of $^{8}/_{6}$, 15 and 13 of $^{9}/_{7}$, 19 and $9^{2}/_{2}$ of $^{10}/_{8}$, 12 and $11^{3}/_{2}$ of $^{9}/_{6}$, 10 and 8 of $^{10}/_{7}$. Together $120^{6}/_{2}$ metatopic against 124 $^{6}/_{2}$ eutopic overlappings.

8. *Ranunculus Flammula.* Observed 50 flowers. Cases of aestivation: 1 eutopic, 9 metatopically quincuncial, 15 vicinal, 20 distal, 1 SW, 1 LW, 3 mixed. Metatopies, counted separately for flowers 1—25 and 26—50: $11^{1}/_{2}$ and $15^{1}/_{2}$ cases of $^{8}/_{6}$, 16 and 15 of $^{9}/_{7}$, 10 and 12 of $^{10}/_{8}$, $9^{1}/_{2}$ and 9 of $^{9}/_{6}$, $8^{1}/_{2}$ and 15 of $^{10}/_{7}$. Together $120^{4}/_{2}$ metatopic against $126^{4}/_{2}$ eutopic overlappings.

9. *Stellaria Holostea.* Observed 10 flowers. Cases of aestivation: 2 metatopically quincuncial, 4 vicinal, 3 distal, 1 SW. Metatopies: 5 cases of $^{8}/_{6}$, 7 of $^{9}/_{7}$, 7 of $^{10}/_{8}$, 4 of $^{9}/_{6}$, 4 of $^{10}/_{7}$. Together 27 metatopic against 23 eutopic overlappings.

10. *Cerastium triviale.* Observed 50 flowers. Cases of aestivation: 5 eutopic, 15 metatopically quincuncial, 15 vicinal, 11 distal, 2 SW, 1 LW. Metatopies, counted separately for flowers 1—25 and 26—50: 15 and 17 cases of $^{8}/_{6}$, 10 and 13 of $^{9}/_{7}$, 11 and 13 of $^{10}/_{8}$, 9 and 19 of $^{9}/_{6}$, 4 and 11 of $^{10}/_{7}$. Together 122 metatopic against 128 eutopic overlappings.

§ 4. PLANTS WITH A TENDENCY TO EUTOPY AT SOME EDGES WHILE AT ONE OR MORE OTHER EDGES THE METATOPIC OVERLAPPINGS PREVAIL.

11. *Echeveria carunculata.* Observed 50 flowers from cincinni. Cases of aestivation: 38 metatopically quincuncial, 8 vicinal, 4 distal. Metatopies, counted separately for flowers 1—25 and 26—50: 0 and 1 cases of $^{8}/_{6}$, 1 and 2 of $^{9}/_{7}$, 25 and 25 of $^{10}/_{8}$, 6 and 5 of $^{9}/_{6}$, 15 and 7 of $^{10}/_{7}$. Together 87 metatopic against 163 eutopic overlappings.

Conclusion. If we knew only the relation 87:163 we might conclude on a general tendency to eutopy. Yet the overstrong preponderance of metatopically quincuncial aestivation is already an indication of particular conditions, and the relations of the different edges definitely show that the tendency to eutopy is very strong only at the edges 6—8 and 7—9, weaker at 6—9, absent at 7—10, whereas at the edge 8—10 an absolutely predominating tendency to metatopy is to be observed.

12. *Cotyledon gibbiflorus.* Observed 50 flowers from cincinni. Cases of aestivation: 10 metatopically quincuncial, 8 vicinal, 32 distal. Metatopies, counted separately for flowers 1—25 and 26—50: 8 and 7 cases of $^{8}/_{6}$, 2 and 2 of $^{9}/_{7}$, 16 and 16 of $^{10}/_{8}$, 23 and 24 of $^{9}/_{6}$, 0 and 0 of $^{10}/_{7}$. Together 98 metatopic against 152 eutopic overlappings.

Conclusion. Analogous to the preceding case; a strong tendency to eutopy at the edges 7—9 and 7—10, a weaker one at 6—8; a very strong tendency to metatopy at 6—9 and probably a weak one at 8—10.

13. *Oliveranthus (Echeveria) elegans*. Observed 25 flowers from cincinni. Cases of aestivation: 5 eutopic, 13 metatopically quincuncial, 7 distal. Metatopies: 2 cases of $8/6$, 6 of $9/7$, 19 of $10/8$, 7 of $9/6$, 3 of $10/7$. Together 37 metatopies against 88 eutopic overlappings.

Conclusion. A marked tendency to eutopy at all edges except 8—10 where metatopy prevails.

14. *Echeveria aurea*. Observed 25 flowers from cincinni. Cases of aestivation: 2 metatopically quincuncial, 5 vicinal, 18 distal. Metatopies: 3 cases of $8/6$, 10 of $9/7$, 23 of $10/8$, 21 of $9/6$, 2 of $10/7$. Together 59 metatopies against 66 eutopic overlappings.

Conclusion. A strong tendency to eutopy at the edges 6—8 and 7—10 and a strong tendency to metatopy at the edges 6—9 and 8—10.

15. *Echeveria glauca*. Observed 50 flowers from cincinni. Cases of aestivation: 3 eutopic, 10 metatopically quincuncial, 17 vicinal, 17 distal, 1 SW, 2 LW. Metatopies, counted separately for flowers 1—25 and 26—50: 11 and 7 cases of $8/6$, 12 and 10 of $9/7$, 14 and 15 of $10/8$, 20 and 11 of $9/6$, 2 and 10 of $10/7$. Together 112 metatopic against 138 eutopic overlappings.

Conclusion. Somewhat like the preceding cases, though much less pronounced. Evidently the aestivation is determined for the greater part by chance. The edge 7—10 is somewhat more eutopic, 6—8 probably too, 8—10 somewhat metatopic.

16. *Erodium gruinum*. Observed 150 flowers, 1—50 indiscriminately taken as the plants produced them, 51—150 only from two-flowered inflorescences, the first flowers of these inflorescences being united into the groups 51—75 and 101—125, the second flowers into the groups 76—100 and 126—150. Cases of aestivation: 1 eutopic, 26 metatopically quincuncial, 45 vicinal, 67 distal, 5 SW, 6 LW.

Metatopies:	$8/6$	$9/7$	$10/8$	$9/6$	$10/7$
Flowers 1— 25	18	6	10	15	20
26— 50	20	5	9	11	14
51— 75	21	10	12	7	21
76—100	23	5	10	11	12
101—125	19	6	9	13	21
126—150	20	6	7	8	18
1—150	121	38	57	65	106

Together 387 metatopic against 363 eutopic overlappings.

4

Conclusion. The individual edges show strong and rather constant differences from each other. At 7—9 there is a clearly marked tendency to eutopy, at 8—10 probably a weak one ; at 7—10 and especially at 6—8 there is a clearly marked tendency to metatopy. The reason for the separate treatment of the first and second flowers will be dealt with in § 5 ; as we see the aestivation is the same in both groups.

17. *Nicandra physaloides.* Observed 7 flowers terminal to the main axis of the plants and 50 flowers from cincinni, 25 right[1]) and 25 left flowers. Cases of aestivation : terminal flowers 3 metatopically quincuncial, 4 distal ; lateral flowers 2 eutopic. 34 metatopically quincuncial, 6 vicinal, 8 distal. Metatopies, counted separately for the main flowers, the left flowers and the right flowers : 0, 7 and 5 cases of $^8/_6$, 5, 19 and 19 of $^9/_7$, 5, 17 and 19 of $^{10}/_8$, 5, 18 and 13 of $^9/_6$, 2, 17 and 14 of $^{10}/_7$. Together 165 metatopic against 120 eutopic overlappings.

Conclusion. At the edge 6—8 there is a marked tendency to eutopy ; at 7—9 and 8—10 to metatopy ; at 6—9 and 7—10 perhaps a weak tendency to metatopy.

§ 5. DISCUSSION.

The facts related in our first paragraph on the plants with an evenly distributed tendency to eutopic overlapping will not give rise to much discussion.

As we know instances of plants with a regularly prevailing eutopic corolla aestivation, it is but natural to assume that in other plants the spiral origin of the corolla becomes partly obscured by the whorl-forming factors and gives rise to a weaker or stronger tendency to eutopy.

It is clear that when in other plants the original differences in position are still more obscured, this will lead towards a complete loss of the tendency to eutopy ; the ideal case being the 50 : 50 relation between the two kinds of overlapping.

This was realized as far as the observations allow us to conclude in the plants of our § 3, a further discussion of which therefore would be superfluous. Only two remarks may follow here about these plants, the first being that we had two Ranunculus spp. amongst them, about which it has never been doubted that the corolla has a spiral origin, a fact which has been fully confirmed again by the researches of HIRMER (25) and SCHÖFFEL (42).

Yet in the older corolla there is no trace whatever of the spiral origin left, so that we have a good example of the levelling power of the whorl-forming factors.

The second remark is that we have two examples of Caryophyllaceous plants in the same paragraph, both belonging to the *Alsineae*, about which

---

[1]) Flowers are called right here when they belong to the flower row at the observer's right, the cincinnus being kept horizontal, its flowers up and the cincinnus apex towards the observer.

EICHLER reports that the corolla aestivation usually is vicinal, especially in that form which arises from contort SW when petal 6 becomes wholly overlapping. Beyond any doubt EICHLER's statement is correct for many cases, but in the two species examined here the aestivation belongs decidedly to a pure chance type.

Besides these cases requiring little discussion, there are the plants of § 2 and § 4 which show very remarkable relations, fully deserving a closer examination.

In § 2 it was eutopy at four edges and an approach to a 50 : 50 relation at the fifth; it would of course be very interesting to know something about the causes leading to such a curious distribution.

Now it is remarkable that in all three cases, furnished by very different families, it is the edge 8—10 which no longer betrays the tendency to eutopy. If this is corroborated by further facts this may lead the way to an explanation; I shall return to this point presently, but I want first to say some words on the cases of § 4.

The plants of § 4 all show another, equally interesting phenomenon, namely that one or more of the edges show a preponderance of metatopy, sometimes to a very high degree.

Now it is clear that while a 50 : 50 relation may be explained by the loss of influence of the original spiral, a tendency to metatopy can only be explained by the assumption of special forces.

Once this is established, the question may be put, whether the 50 : 50 relation at the edge 8—10 of § 2 may not be caused in the same way, not by loss of influence of the spiral, but by an equipoise between the spiral and the supposed special forces.

In order to get some light on this question, we may first compare the distribution and the strength of the different tendencies to eutopy and to metatopy in the following way.

	6— 8	7—9	8—10	6—9	7—10
11. Echeveria carunculata	+ +	+ +	– –	+	
12. Cotyledon gibbiflorus	+	+ +	– ?	– –	+ +
13. Oliveranthus elegans	+	+	–	+	+
14. Echeveria aurea	+		–	–	+
15. E. glauca	+ ?			– ?	+
16. Erodium gruinum	– –	+ +	+	+ ?	– –
17. Nicandra physaloides	+	–	–	– ?	– ?

In this table +? denotes a probable tendency, + a more pronounced tendency and + + a very strong tendency to eutopy; —?, — and — — indicate in the same way an increasing tendency to metatopy.

The comparison makes it immediately clear that the five examples of

Crassulaceae 11—15 have much in common and that 16 and 17 are very different from them; in the *Crassulaceae* examined here 6—8 and 7—10 tend to eutopy, whereas the tendency to metatopy is striking in 8—10; it is only 6—9 that behaves differently in the different species.

When now we remember that 8—10 was the particular edge in the cases of our § 2, we cannot fail to get the impression that the tendency to metatopy in 8—10 here is due to the same factor that neutralized the original eutopic tendency in the plants of § 2.

The factors causing such a metatopy are of course entirely unknown: we can only make guesses as to their nature.

We may first remark that these causes may be either strictly local, and may be limited to a single petal, or they may have a wider field of action and may affect a certain side of the flower.

Local influences may be supposed to emanate from the highest phyllomes under the flower, from prophyll β in lateral flowers or from the highest bract or foliage leaf in terminal flowers. The highest of these phyllomes, whether prophyll or bract or leaf, is placed more or less exactly under petal 8; a local influence might therefore be expected in the first place in the neighbourhood of this petal. The next lowest phyllome, prophyll α or whatever it may be, is situated under petal 7, or near to it.

Influences with a wider field may be due to a subzygomorphy, a phenomenon which is not rare in flowers.

Both kinds of influences, the local and the general, may of course be of any kind: furthering or repressing. In literature they have been abused on a large scale, as they have the great attraction of being able to "explain" anything one may want, in more or less physiological terms. A lower phyllome may further a higher one by providing it with good vascular connections; it may repress it as well by withdrawing all available nutritive substances; it may act mechanically by pressures, etc. All these suppositions are entirely speculative and at present cannot be checked; we had therefore better only state the facts and hope for some more information about the physiological causes in future.

These facts are here: in the examined *Crassulaceae* a remarkable tendency to metatopy at the edge 8—10 which may be caused by a repression of 8, perhaps by prophyll β or the highest leaf; the same factor seems to be present but weaker in *Passiflora coerulea, Candollea cuneiformis* and *Rosa canina*.

In *Erodium gruinum* and *Nicandra physaloides* the conditions may be described otherwise: for *Erodium* as a furthering of 8 and 10, or a furthering of that side of the flower, for *Nicandra* as a furthering of petal 8 and 9.

With the assumption of such furthering or repressing factors, however obscure their nature may be, we are on a safe foundation, as we may observe them on a large scale in any zygomorphic flower, in all floral belts.

CHAPTER 6.

Observations on plants with zygomorphic corolla aestivation.

The observed species will be dealt with in three paragraphs, treating respectively the plants with descendent, ascendent and confluent aestivation.

§ 1. SPECIES WITH DESCENDENT COROLLA AESTIVATION.

18. *Scrophularia nodosa.* Observed 125 flowers, 1—25 being terminal to the lateral inflorescence axes, 26—125 being taken higher up in the lateral cincinni.

The corolla aestivation is strictly descendent; the two erect petals 7 and 10 at the back side of the flower show a clear overlapping, one covering the other.

A distinct disadvantage of the plant is that the calyx aestivation disappears long before the corolla aestivation sets in. We have therefore to determine the calyx spiral from the place in the inflorescence. According to WYDLER (64, p. 411) the cincinnus is from β, so that in every cincinnus the left flowers (for definition see footnote on p. 50) have their α on their left; and as sep. 2 is turned towards the axis, the left flowers have petal 7 at the left and 10 at the right.

Determining the 7—10 overlapping from these premises I observed $7/10$ in the main flowers 10 times, in the lateral 45 times, $10/7$ 15 and 55 times. This might seem to represent a chance distribution with an unimportant preponderance of metatopy.

When we treat the right and left flowers separately (and the main flowers with the same prophyll position), the aspect changes altogether. We then get the following survey.

	Left flowers		Right flowers	
	$7/10$	$10/7$	$7/10$	$10/7$
1— 25	4	10	6	5
26— 50	3	8	11	3
51— 75	3	8	9	5
76—100	0	10	7	8
101—125	3	10	9	3

We see that in the main flowers as well as in the lateral flowers there is a certain contrast between the right and the left flowers: in the left flowers we observe a strong tendency to metatopy in the median plane (13 eutopic against 46 metatopic), in the right flowers a marked tendency to eutopy (42 eutopic against 24 metatopic cases).

This remarkable contrast may evidently be described as follows: the petals 7 and 10 have a strong tendency to a right-handed autotropical contortion in the symmetry plane. Altogether there were 88 cases of right-handed contortion against 37 left-handed.

This result, though not serviceable for the examination of the remains of the original spiral, yet is very instructive as an illustration of the various ways the corolla aestivation may be influenced.

19. *Viola cornuta,* a blue-flowering garden variety. Observed 100 flowers. The aestivation being strictly descendent, only the edge 7—10 in the symmetry plane has been recorded. In open flowers and already in advanced buds the calyx spiral is no longer to be determined, as the corolla spur soon protrudes between sepals 1 and 3. All flowers were therefore observed in the young bud stage. The overlapping in the median plane happened to be exactly 50 times $7/_{10}$ and 50 times $10/_7$, the relations being in the successive lots of 25 flowers 8 : 17, 14 : 11, 16 : 9 and 12 : 13.

Conclusion. A chance overlapping in the median plane.

20. *Viola cornuta,* a yellow-flowering garden variety. Observed 150 flowers. The overlappings in the median plane were 61 eutopic against 89 metatopic cases, the relation in the successive lots of 25 flowers being 6 : 19, 12 : 13, 7 : 18, 10 : 15, 11 : 14 and 15 : 10.

The expectation would have been 75 ± 4.1 for eutopic and metatopic, if the distribution were only due to chance; the deviation of 14 cases being nearly $3\frac{1}{2}$ times the probable error. So a certain tendency to metatopy may have been present.

21. *Viola tricolor.* Observed 25 flowers; of $7/_{10}$ 12 and of $10/_7$ 13 cases: a chance distribution.

22. *Pelargonium zonale,* garden variety *Paul Grampel.* Observed 100 flowers. Cases of aestivation: 6 metatopically quincuncial, 33 vicinal, 60 distal, 1 mixed.

According to EICHLER the aestivation of the *Pelargonium* corolla is a "nach Labiatenweise absteigende Präfloration"; this is of course a distal one. And as our distal cases mostly were descendent, the species is treated here and not in our chapter on variably imbricate aestivation.

To get a better survey of the phenomena I may refer to the following tables.

	Aestivation in the anterior half (petals 8—6—9)			
	descendent $(^8/_6, \ ^9/_6)$	S W $(^8/_6, \ ^6/_9)$	L W $(^6/_8, \ ^9/_6)$	ascendent $(^6/_8, \ ^6/_9)$
1— 25	12	8	3	2
26— 50	6	12	4	3
51— 75	12	10	2	1
76—100	16	9	0	0

	Lateral aestivation (7—9, 8—10)			Median plane (7—10)		
	descendent $(^7/_9, \ ^{10}/_8)$	different at both sides	ascendent $(^9/_7, \ ^8/_{10})$	$^7/_{10}$	$^{10}/_7$	mixed
1— 25	22	2	1	23	2	0
26— 50	25	0	0	17	8	0
51— 75	25	0	0	18	6	1
76—100	25	0	0	16	9	0

From these figures we may learn first that there is a marked tendency to eutopy in the median plane, 74 against 25 cases.

Further we see that the aestivation on the right and left side of the flower is almost without exception descendent.

On the front side we observe however a curious mixture of descendent aestivation (46 cases) and heterotropic aestivation (39 cases), the remaining 9 cases of LW and 6 of ascendent aestivation being obviously real casual deviations.

In view of the many near relatives of *Pelargonium* with heterotropic corolla aestivation the occurrence of a vestige of it in this case is not to be wondered at.

23. *Tropaeolum maius.* Observed 50 flowers. Cases of aestivation: 45 vicinal, 3 distal, 2 mixed.

The very rare occurrence of a corolla with practically only a vicinal aestivation is due to the fact that the aestivation in the anterior half of the flower is heterotropic, that of the posterior half descending (cf. 13, p. 283; 38; 15, p. 284; 46, p. 1081). Metatopies, counted separately for flowers 1—25 and 26—50: 25 and 25 cases of $^8/_6$, 0 and 0 of $^9/_7$, 25 and 25 of $^{10}/_8$, $^1/_2$ and 0 of $^9/_6$, 3 and 1 of $^{10}/_7$.

Conclusion. The descending aestivation is responsible for the fixed

metatopy at 8—10, and for the equally strong eutopy at 7—9; the hetero-
tropy for the perfect metatopy at 6—8 and the nearly perfect eutopy at
6—9; the overlapping at the edge 7—10 is not affected by the descending
tendency, perhaps by the heterotropy. In any case it is eutopic with
remarkable constancy, in 46 against 4 cases.

24.   *Tropaeolum peregrinum.*   Observed 25 flowers. Aestivation open
at all edges but for 7—10; the inclusion of this species into this paragraph
is only to be condoned by appealing to the relation to *Tr. maius.* In all
25 observed flowers the overlapping was $^7/_{10}$.

§ 2.   PLANTS WITH ASCENDENT COROLLA AESTIVATION.

25.   *Pelargonium zonale,* garden variety *Van Ries.* Observed 100
flowers. Cases of aestivation: 2 eutopic, 16 metatopically quincuncial,
39 vicinal, 41 distal, 2 SW.

The great and quite unexpected difference of this variety from the one
described in the preceding paragraph under N⁰. 22 is felt already in this
aestivation distribution where the distal form no longer predominates as
was the case there. The difference is revealed however much more clearly
by the following survey.

	Aestivation in the anterior half (petals 8—6—9)			
	descendent ($^8/_6$, $^9/_6$)	S W ($^8/_6$, $^6/_9$)	L W ($^6/_8$, $^9/_6$)	ascendent ($^6/_8$, $^6/_9$)
1— 25	3	19	0	3
26— 50	1	19	3	2
51— 75	2	11	4	8
76—100	2	18	1	4

	Lateral aestivation (7—9, 8—10)			Median plane (7—10)	
	descendent ($^7/_9$, $^{10}/_8$)	different at both sides	ascendent ($^9/_7$, $^8/_{10}$)	$^7/_{10}$	$^{10}/_7$
1— 25	6	9	10	10	15
26— 50	6	10	9	9	16
51— 75	7	10	8	10	15
76—100	2	9	14	10	15

We see that the eutopy in the median plane of the former variety is replaced here by a preponderance of metatopy; 39 eutopic against 61 metatopic cases, the deviation from the 50 : 50 relation being about three times the probable error.

The descendent aestivation on both sides of the flower gives place here to a certain preponderance of ascendent aestivation (41 against 21 cases and 38 mixed cases).

On the front side we find instead of the mixture of descendent and heterotropic aestivation a preponderance of the same heterotropy, mixed with a much weaker ascendent aestivation.

26. *Delphinium villosum* var. *tiroliense* [1]). Observed 25 flowers. Aestivation of the four developed petals ascendent, as mentioned by EICHLER (17, II p. 166); as the four developed petals must bear the numbers 12, 7, 10 and 13 according to my notation, the ascendent aestivation amounts to the metatopic overlappings $^{12}/_7$ and $^{13}/_{10}$.

In the median plane all flowers showed the overlapping $^7/_{10}$.

27. *D. elatum*. Observed 25 flowers. Aestivation of the four developed petals not ascendent, but throughout eutopic: $^7/_{12}$, $^7/_{10}$ and $^{10}/_{13}$ in all flowers. The lateral petals 12 and 13, though overlapped at their posterior edge by 7 and 10, both show a longitudinal plait in their anterior half, more or less overlapping again the adjoining petal 7 or 10.

28. *D. bicolor*. Observed 25 flowers. Lateral aestivation eutopic in all flowers; in the median plane 23 cases of $^7/_{10}$ and 2 of $^{10}/_7$.

29. *D. Turkestanicum*. Observed 25 flowers. Lateral aestivation eutopic in all cases; in the median plane 23 cases of $^7/_{10}$ and 2 of $^{10}/_7$.

30. *Cassia floribunda*. Observed 25 flowers. Aestivation in all cases ascendent; because of the peculiar mode of calyx junction of the *Caesalpiniaceae* the median edge of the corolla is the anterior one 6—9. In all flowers this edge showed eutopic overlapping $^6/_9$; this is the same result as obtained by the BRAVAIS brothers for *Cercis*.

§ 3. PLANTS WITH CONFLUENT COROLLA AESTIVATION.

31. *Aesculus Hippocastanum*. Observed 300 flowers, 150 from the big tree in the Groningen Botanic Gardens, 150 from another tree in a municipal park. Corolla aestivation more or less confluent along the skew symmetry plane through sepal 4. Petal 8, lying opposite 4 in the symmetry plane at the "anterior" side, is often badly developed or even deficient,

---

[1]) For the determination of Nos. 26 and 27 I am indebted to my colleague Prof. B. H. DANSER.

6 and 10 are lateral, 7 and 9 lie at the back side, the edge 7—9 falling in the symmetry plane.

a. Hortus tree.

	Metatopies and open edges:									
	$8/6$	$6\|\|8$	$9/7$	$7\|\|9$	$10/8$	$8\|\|10$	$9/6$	$9\|\|6$	$10/7$	$7\|\|10$
1— 25	9	6	7 $2/2$	0	10	7	3	0	24	0
26— 50	9	11	7 $3/2$	0	7	7	0	0	25	0
51— 75	9	10	11 $3/2$	0	5	10	0	1	24	1
76—100	4	17	13	0	6	16	0	0	24	0
101—125	9	8	11 $2/2$	0	7	8	$2^1/2$	0	25	0
126—150	8	11	12 $4/2$	0	8	9	0	0	24	0
1—150	48	63	61 $14/2$	0	43	57	$5^1/2$	1	146	1
Eutopic:	39	—	75 $14/2$	—	50	—	$143^1/2$	—	3	—

The aestivation is therefore strongly confluent at the edges 6—9 and 7—10; the edges 6—8 and 8—10 on the contrary not only are very often open by lack of a well developed petal 8, but moreover are variably imbricate.

The edge 7—9 in the symmetry plane is also variably imbricate, with a quite insignificant preponderance of eutopy.

b. Park tree.

	Metatopies and open edges:									
	$8/6$	$6\|\|8$	$9/7$	$7\|\|9$	$10/8$	$8\|\|10$	$9/6$	$9\|\|6$	$10/7$	$7\|\|10$
1— 25	5	10	21 $2/2$	1	8	9	0	0	25	0
26— 50	5	10	13 $3/2$	0	6	10	1	0	24	0
51— 75	$10^1/2$	10	16 $1/2$	0	6	10	1	0	24	0
76—100	3	17	15 $1/2$	1	5	16	0	0	25	0
101—125	4	12	13 $3/2$	$1/2$	7	12	0	0	25	0
126—150	7	12	13 $2/2$	1	4	13	1	0	25	0
1—150	$34^1/2$	71	91 $12/2$	$3^1/2$	36	70	3	0	148	0
Eutopic:	$44^1/2$	—	43 $12/2$	—	44	—	147	—	2	—

As in the former tree the edges 6—9 and 7—10 are confluent, the edges 6—8 and 8—10 are often open and further variably imbricate: the median edge 7—9 on the contrary shows decidedly a preponderance of metatopy.

32. *A. flava* var. *discolor*. Observed 50 flowers. Only four petals developed owing to the abortion of 8; aestivation confluent, as all flowers show the overlappings $6/9$ and $10/7$. In the symmetry plane the two lots of 25 flowers had 20 and 22 cases of $9/7$, and 5 and 3 of $7/9$, so that the metatopic overlapping strongly prevailed.

33. *A. Pavia*. Observed 50 flowers. Four petals developed as in N⁰. 32, and the same confluent aestivation. In the symmetry plane the overlapping in the two lots of 25 flowers was in 21 and 21 cases $9/7$, in 4 and 3 $7/9$, in 0 and 1 open. As in the preceding case therefore the metatopy prevailed strongly.

§ 4. DISCUSSION.

When we first pay attention to the aestivation outside the symmetry plane, we see that in our material the influence of the zygomorphy on the aestivation may vary in strength, a result which only might have been expected after the survey of the calyx aestivation in Chapter 4, § 1.

The aestivation was perfectly ascendent in *Scrophularia, Viola, Tropaeolum* and in *Delphinium villosum*, and perfectly descendent in *Cassia*: in *Pelargonium zonale* var. *Paul Grampel* the descendent aestivation was somewhat laxer as it was mixed at the anterior side of the flower with heterotropic contortion; finally in the var. *Van Ries* of the same species we had a very lax ascendent aestivation, mixed at the anterior side with a preponderant heterotropy.

In *Aesculus Hippocastanum* we had a species, with a more or less confluent aestivation mixed with a certain amount of variable imbrication.

Coming now to the results obtained in the symmetry plane, the conditions were equally different in the different species.

A perfect tendency to eutopy was observed in the examined species of *Tropaeolum*, of *Delphinium* and in *Cassia floribunda*; and from literature [1]) we may add the case of *Cercis* of the BRAVAIS brothers.

A preponderance of eutopy was found in *Pelargonium zonale* var. *Paul Grampel*.

A variably imbricate condition was observed in *Viola cornuta* with blue

---

[1]) The manuscript of this paper having been completed I came across the most excellent paper by AL. BRAUN on *Delphinium* (4) in which on the basis of a large body of observations is stated for several *D.* species (*Cardiopetalum, grandiflorum* and others) that the two petals 2 and 5 (our 7 and 10) nearly always show a eutopic aestivation, as reported here.

flowers, in *V. tricolor* and in one of the two trees of *Aesculus Hippo-castanum*.

A weak tendency to metatopy was perhaps shown by the *Viola cornuta* with yellow flowers and by *Pelargonium zonale* var. *van Ries*; a somewhat stronger tendency by the other tree of *Aesculus Hippocastanum*, and a striking tendency to metatopy by *Aesculus flava* and *Pavia*.

Finally one species, *Scrophularia nodosa*, was remarkable by its tendency to right-handed contortion in the symmetry plane.

The explanation of these different conditions would have been of a rather simple nature if we had only met with a tendency to eutopy, a variably imbricate aestivation and a tendency to contortion; the first would have been a remnant of the original spiral, the second the loss of it and the third would fall in with the cases to be described in our next chapter.

We have however several species with a more or less pronounced tendency to metatopy of the symmetry plane aestivation. This unexpected result is too pronounced, at least in the *Aesculus* spp., to be ignored. It may perhaps be explained in the following way.

In the *Aesculus* flower the two petals 7 and 9 occupy similar places with regard to the symmetry plane, but their positions with regard to the cincinnus as a whole are quite different, petal 9 being situated at the free side, 7 being turned towards the other flower row.

It is therefore quite possible that 9 is furthered as compared with 7, just as the floral parts towards the circumference of many umbels may be furthered. And such a furthering of 9 might easily change the over-lapping at the edge 7—9.

In *Pelargonium zonale* var. *van Ries* an analogous explanation may be brought forward for the prevailing overlapping of 10 over 7, petal 10 being situated at the side of the fertile β prophyll. Such a furthering of the β-side of a flower is for example to be observed in a very striking form in the flowers of the *Valerianaceae*.

For the doubtful tendency to metatopy in *Viola cornuta*, if it was confirmed by further observations, such an explanation would not be available.

If the above explanations for a tendency to metatopy should be right, we might ask whether the tendencies to eutopy are still conclusive evidence for the spiral construction of the flower; when a tendency to metatopy may be explained by influences from the outside, a tendency to eutopy might be due in the same way to other external agencies.

The validity of this objection is not to be denied: surely the cogency of the argument of the eutopic aestivation is diminished in this way. Yet I believe that not all the conclusive force is taken away.

For in the first place the cases of tendency to eutopy were not only more numerous in my material than those of tendency to metatopy, but the eutopy itself too was much stronger. Besides, and this is perhaps the

best argument, the tendency to metatopy was present in inflorescences of a cymose type with furthering from β whereas the tendency to eutopy was observed in single flowers or in simple racemes where the presence of influences such as may exist in cincinni is much less to be expected.

In the cases of the *Delphinium* spp, where the flower is admittedly spiral (cf. EICHLER 17, II, p. 166, SCHÖFFEL 42, p. 368) the eutopic aestivation without any doubt is due to the presence of the original spiral. Yet the corolla is so strongly dorsiventral as to be developed only in the posterior half and the lateral aestivation in some species is regularly metatopical owing to the zygomorphy influence.

In view of these facts the similar eutopic aestivation in the symmetry plane in *Tropaeolum, Cercis* and *Cassia* seems to me to have to be explained in the same way.

CHAPTER 7.

Observations on plants with contort corolla aestivation.

§ 1. PLANTS WITH AUTOTROPIC COROLLA AESTIVATION.

As it was not easy to obtain sufficient material of species which were suitable for the examination I must confine myself to the mention of two species only, one of which hardly deserves mentioning as the number of observed deviations was very small.

34. *Phlox paniculata.* Corolla right contort. As the sepals do not overlap each other and do not show their genetic spiral in any other way, the petal numbers had to be derived from the order of the preceding phyllomes.

For sake of convenience I only examined lateral flowers with two prophylls, i.e. the main flowers of the higher lateral axes of the panicle and the α-flowers of the dichasial parts; from the position of these prophylls the sepals and petals could easily be numbered; the β-prophyll being inserted higher and subtending a flower without prophylls.

Observed 147 flowers, 71 with a right calyx spiral and the prophyll at their right, and 76 with a left calyx spiral. Of the 71 right-handed 50 were wholly contort SW, 21 showing the following faults: 3 of $6/8$, 7 of $7/9$, 12 of $8/10$, 3 of $9/6$ and 4 of $10/7$. Together 22 rational and 7 irrational faults.

The 76 flowers with a left-hand spiral were contort LW in 54 cases, 22 showing the following faults: 8 of $8/6$, 4 of $9/7$, 3 of $10/8$, 8 of $6/9$ and 4 of $7/10$. Together 12 rational and 15 irrational faults; a chance distribution would have given for 29 faults in right-handed flowers and 27 in left-handed the relations $17.4:11.6$ and $10.8:16.2$. The rational faults in our case were therefore slightly in advantage in both lots, but not so as to allow of any other conclusion than that of a chance distribution.

35. *Myosotis palustris.* Corolla right contort. Observed 50 flowers, 47 being perfectly contort. The remaining three showed four faults, two rational and two irrational ones: distribution perhaps at random.

§ 2. PLANTS WITH HETEROTROPIC COROLLA AESTIVATION.

36. *Plumbago Larpentae.* Observed 121 flowers. Cases of corolla aestivation: 1 metatopically quincuncial, 21 vicinal, 4 distal, 85 contort SW. Upon a nearer examination of 15 of these 26 aberrant flowers the following faults against SW contortion were observed: 3 cases of $6/8$, 5 of $7/9$, 4 of $8/10$, 4 of $9/6$ and 5 of $10/7$.

The distribution of these faults evidently is at random.

37. *Pl. Capensis.*   Observed 53 flowers. Cases of corolla aestivation: 3 vicinal, 50 contort SW. The three aberrant flowers had two rational faults, one irrational. As far as the very small number of deviations goes, the distribution may be at random.

38. *Geranium nodosum.*   Observed 100 flowers. Cases of aestivation: 4 metatopically quincuncial, 26 vicinal, 70 contort SW. Faults against SW contortion: 3 cases of $6/8$, 11 of $7/9$, 11 of $8/10$, 3 of $9/6$, 7 of $10/7$. The distribution is evidently at random; in 35 faults the numbers of rational and irrational should be on the average 21 : 14. Observed 25 : 10.

39. *Geranium sanguineum.*   Observed 300 flowers in three lots of 100, at different times. As the results were in some respects very different, I may mention that I picked the flowers from the same plant bed, 1—100 on 13—14 July 1931, 101—200 from 25 Aug.—1 Sept. 1932, 201—300 from 18 May—6 June 1933.

The cases of aestivation in these three lots were:

Flowers	1—100	101—200	201—300
Eutopic	4	4	1
Metat.. quincunc.	8	18	16
Vicinal	39	21	31
Distal	15	26	49
Contort S W	25	24	3
Contort L W	0	1	0
Open or spoiled . . .	9	6	0

The difference between these lots can already be gathered from the percentage of contort cases which drops from 25 to 3, so that the last lot is no longer contort at all.

The detailed survey of the following table however reveals the difference much better.

In the first lot of 100 flowers the rational prevail strongly over the irrational faults; relation 92 : 11, quite removed from mere chance. (Chance relation in 103 faults on the average 61.8 : 41.2).

In the second lot the preponderance is much weakened to a 107 : 45 relation (chance relation in 152 faults being 91.2 : 60.8).

In the third lot it has completely vanished, the relation being 122 : 83 (chance relation in 205 faults 123 : 82).

Conclusion.   In this plant there may be sometimes a marked preponderance of rational over irrational faults, at other times the preponderance may be absent.

Flowers	Faults against S W contortion				
	$^6/_8$	$^7/_9$	$^8/_{10}$	$^9/_6$	$^{10}/_7$
1— 25	11	5	6	1	0
26— 50	6	2	10	0	3
51— 75	6	7	11	0	3
75—100	12	2	14	2	2
1—100	35	16	41	3	8
101—125	10	5	12	8	4
126—150	9	5	10	6	5
151—175	10	7	11	5	5
176—200	11	5	12	4	8
101—200	40	22	45	23	22
201—225	12	9	8	19	4
226—250	16	9	9	17	5
251—275	20	8	9	16	2
276—300	13	0	9	14	6
201—300	61	26	35	66	17
1—300	136	64	121	92	47

40. *Geranium pratense.* Observed 100 flowers. Cases of aestivation :
4 eutopic, 18 metatopically quincuncial, 35 vicinal, 23 distal, 19 SW,
1 mixed; in all a mixture of contort SW and variable imbrication.
Observed deviations :

Flowers	Faults against S W contortion				
	$^6/_8$	$^7/_9$	$^8/_{10}$	$^9/_6$	$^{10}/_7$
1— 25	17	5	5	4	6
26— 50	15	5	8	6	7
51— 75	14	4	2	6	8
76—100	18	3	7	$3^1/_2$	6
1—100	64	17	22	$19^1/_2$	27

The rational faults somewhat prevail over the irrational: relation 103 : 46½ (chance relation in 150 faults 90 : 60); this result however is only due to the constant large percentage of $^6/_8$ cases. The other edges are all very similar in their conditions.

Conclusion. A lax SW contortion, with a strong tendency to eutopy at the edge 6—8.

41. *Cistus polymorphus.* Observed 100 flowers. Cases of aestivation : 2 metatopically quincuncial, 19 vicinal, 1 distal, 78 contort SW. Observed faults against contortion : 3 cases of $^6/_8$, 5 of $^7/_9$, 15 of $^8/_{10}$, 3 of $^9/_6$, 2 of $^{10}/_7$. Together 23 rational against 5 irrational faults; the prevalence of the rational faults being wholly due to a relatively strong tendency to eutopy at the edge 8—10.

42. *Statice Limonium.* As I had been obliged to make many observations on the corolla aestivation of this species, on behalf of my investigation of the glomerule (49), I tried to use the results for the present purpose.

The great difficulty however was that the calyx does not betray the original spiral by its aestivation, whilst the abortion of part of the prophylls and especially the many turns and shifts much impede the determination of this spiral by other means.

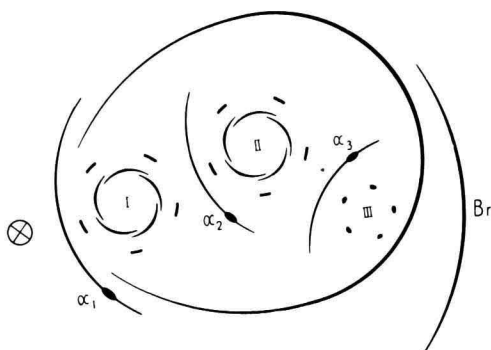Our fig. 7 gives an empirical diagram of the glomerule, copied from my paper on the *Plumbaginaceae* inflorescence (49). We see from it that in the adult flower one sepal is turned towards the parent axis; further we may take for granted that the calyx spiral is emprosthodromous as in the other family members.

Fig. 7. *Statice Limonium.* Empirical diagram of right glomerule.

In order to make the best of my observations, I made moreover two suppositions about the calyx position, suppositions which I take to be rather safe.

One is that sep. 2 originally has been laid down in an adaxial position, as it is the case in nearly all pentamerous emprosthodromous calyces of Dicotyledons; the other is that every flower keeps as much as possible its position with respect to its prophylls; when these prophylls are shifted, the flower is supposed to turn with them, no additional torsion taking place in the pedicel between flower and prophylls.

The twist of flower N⁰. I having been determined (cf. 49) as more than 45° and less than 90°, it follows from the above suppositions that the

5

sepal flower I turns towards the parent axis must be sepal 4; the diagram of the glomerule will make this clear.

Flower II is placed in that case before petal 8 of I; and as II has been turned through somewhat less than 90° in the opposite direction as I, it will be clear that II again turns its sep. 4 towards its parent axis I. Its daughter-flower III is however not placed before its sep. 8, but before its pet. 10, in consequence of the zigzag position of the flowers. In cases where more than three flowers are present, the relation of IV to III is like that of III to II.

Having numbered the petals of the observed flowers after these suppositions, I got the following results.

Aestivation	Flower		Faults against S W	Flower	
	I	II		I	II
Eutopic	0	4	$^6/_8$	11	49
Quincuncial	2	12	$^7/_9$	3	13
Vicinal	14	27	$^8/_{10}$	1	64
Distal	1	44	Rational faults	15	126
Contort S W	186	23	$^9/_6$	2	1
Contort L W	0	0	$^{10}/_7$	6	11
	203	110	Irrational faults	8	12

From this table we see not only that flower I is much more exact in the contortion than II, but we see moreover that in II the relation of rational to irrational faults (126:12) is strongly in favour of the rational ones; out of 23 faults in flower I and 138 in II the average values of a chance distribution would be 13.8:9.2 and 82.8:55.2. For flower I the observed relation is about the same as the chance relation, for II the number of irrational faults is not yet a fourth of what might have been expected.

43. *Goniolimon tataricum*. The description of the glomerule of this species (49) will make it clear that flower I will be in no way serviceable for our purposes by its mixture of heterotropy and anomotropy; any overlapping may be treated as a fault either against contort SW or against LW.

I was therefore the more surprised to find in flower II a quite different condition in which the tendency to contortion was so much weakened as to be no longer discernible, but where eutopy was the prevailing tendency.

The suppositions to be made about the calyx position were the same as for *Statice Limonium*, that sep. 2 had been laid down in an adaxial position

and that II turns its sep. 4 towards I, which may be derived from the analogous position of the prophyll a and the position of flower III, when it is present.

A diagram was recorded for 50 flowers II, 25 from right and 25 from left glomerules, and the petals numbered according to the suppositions. Cases of aestivation: 16 eutopic, 21 metatopically quincuncial, 7 vicinal, 6 distal. Metatopies, counted separately for the left and the right flowers: 1 and 2 cases of $8/6$, 4 and 0 of $9/7$, 13 and 14 of $10/8$, 2 and 6 of $9/6$, 0 and 0 for $10/7$.

As we see there is no trace of contortion left in these figures, and the tendency to eutopy is so strong as to give 16 eutopic corollas on 50 flowers. It is accordingly striking for all edges but for 8—10, where a chance distribution is to be observed.

§ 3. D i s c u s s i o n. The results obtained in our first paragraph on the autotropic corolla need not detain us long as they were only negative. In the only plant of which sufficient data could be gathered the departures from the autotropy towards eutopy and towards metatopy seemed to be distributed only by chance.

In our second paragraph on the heterotropic corolla we met with some similar cases, namely in the two *Plumbago* spp. and in *Geranium nodosum*.

In two other cases of heterotropic corollas there was a certain tendency to eutopy at one of the five edges, namely in *Geranium pratense* at the edge 6—8 and in *Cistus polymorphus* at 8—10. Of such partial tendencies to eutopy there are probably many more instances in nature; EICHLER mentions the occurrence of a vicinal aestivation in several *Alsineae* of such a form that we may describe it as contort SW with eutopic overlapping at 6—8 (17, II, p. 112).

For these partial tendencies influences presumably are responsible analogous to those we were obliged to assume in so many cases of variable imbrication; in any case the phenomena in both groups of plants will have to be explained on the same lines.

In *Geranium sanguineum* we had the remarkable case of a more general tendency to eutopic deviations from contortion, but this seemed to be present only sometimes, and to be absent at other times of the year.

This curious result seems to point to influences of climatic circumstances, which may easily change the rate or the power of growth; it is quite possible that for example a slower growth may cause a condition where the original spiral order has been completely done away with when aestivation sets in, or something of that kind.

In *Statice Limonium* we had further a case of a strongly developed heterotropy in the flower I corolla, with only few deviations which were distributed at random. In the flower II the corolla heterotropy was only lax, being subject to many faults among which the eutopic faults strongly prevailed.

The only objection against this case is that the determining of the petal numbers was based upon two, for the rest not very risky, suppositions.

Our last plant, Goniolimon was in some respect similar, in so far as the flower II of the glomerule was much less contort; this went however so far here that the corolla even became wholly variably imbricate with a strong tendency to eutopy, no traces of contortion being left. It is very remarkable that the tendency to eutopy was very strong at all edges excepting 8—10, just as in *Passiflora coerulea* and other plants.

General discussion.

The observations recorded in our chapters 5—7 on the variably imbricate, the zygomorphic and the contort corolla having been discussed in the last paragraphs of the chapters, I have to discuss here only two points of a more general interest.

The first of these points is the question whether the one-sided and local influences, assumed in Chapters 5 and 6 as acting on the corolla aestivation, really exist. The other is whether the facts furnish any conclusive arguments as to the spiral origin of the corolla.

As to the first question, in the variably imbricate and in the zygomorphic corollas we had not only to assume the influence of an original spiral, a levelling influence of whorl-forming factors in the variably imbricate, and an influence of the zygomorphy factors in the zygomorphic corollas, but we met with many one-sided influences of another nature, biasing the aestivation in different ways, and even local influences determining the overlapping at one single corolla edge.

The real existence of such influences may perhaps be granted by most botanists for the one-sided influences in zygomorphic flowers which are evident in many other respects too.

But as to the local influences many botanists will be inclined to consider them as a forced makeshift invented to save the spiral construction. Yet we may find other phenomena which are only to be explained by the same assumption of influences of such a kind. To prove this I want to quote here some instances from the excellent paper by WYDLER on the order of dehiscence of anthers (63) which I shall treat on the basis of our Fig. 8, copied from his work.

In Fig. 8 the floral diagrams are given of six plants, A—C representing zygomorphic flowers. The sepals have been numbered according to the genetic spiral, the stamens in the dehiscence order.

In A, *Scrophularia*, we see that the four stamens mature in an ascendent order, contrary to the descendent corolla aestivation, but we see moreover that in each stamen pair the one at the β-side is more advanced. This may be related to the fact that *Scrophularia* has a cincinnus from β.

In C, *Heuchera*, the anthers dehisce in a descendent order, which corresponds to a weakly expressed median zygomorphy with furthering of the back side of the flower; in the pairs it is again the β-side which is in advance; the inflorescence also shows furthering from β.

In B, *Dictamnus*, there are two stamen whorls of which the epipetalous

sheds pollen somewhat earlier, the order being descendent with again a slight furthering of the β-side. The dehiscence pattern in this way becomes
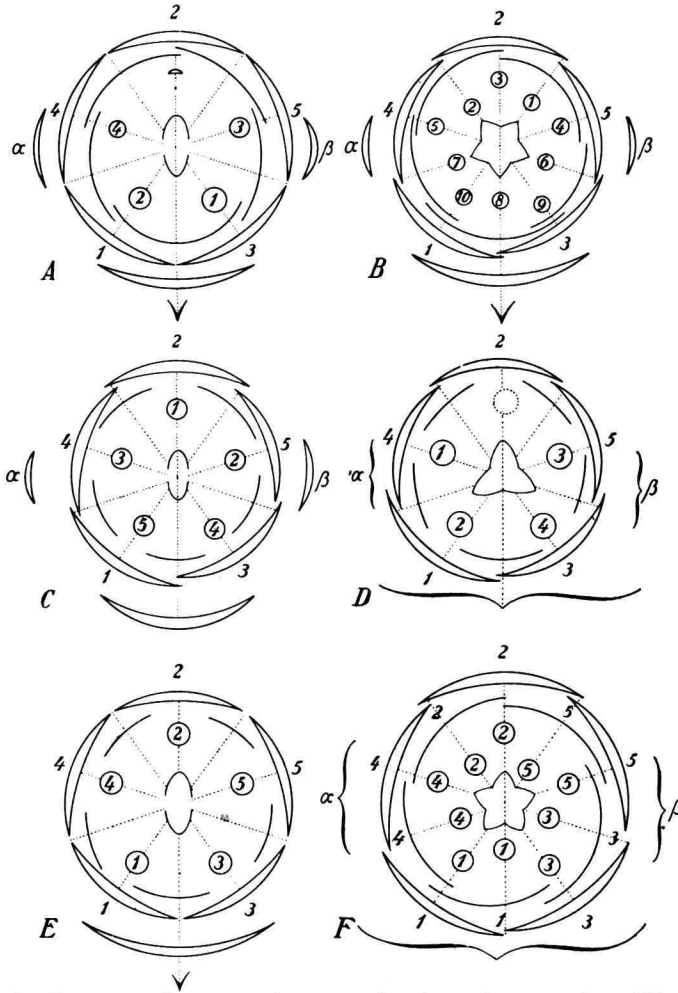

Fig. 8.   Diagrams illustrating the order of anther dehiscence, from WYDLER (61, pl. III—VI). $A =$ fig. 7 of WYDLER, $B = 11$, $C = 10$, $D = 18$, $E = 1$, $F = 3$.

rather complicated, yet with perfectly clear rules. The inflorescence again has furthering from β.

In D—F three actinomorphic flowers are represented. In D, *Stellaria media*, in the case of four stamens, the order is analogous to that of C: descending with a lateral advance. This time it is however not the β-side, but the α-side which is advanced, though the dichasial inflorescence has a certain furthering of the β-prophyll and β-flower.

In E and F the conditions are of another kind; instead of general one-sided influences we observe here numerous well-marked local influences.

E represents the Umbelliferous flower. The anthers here shed in a

spiral order, not in the order of their genetic spiral, but in that of the sepals before which they are placed. This condition is met with, not only in numerous *Umbelliferae*, but moreover in *Chenopodium* (with deviations), *Acroglochin persicarioides, Thisantha glomerata.*

Of course we might think of a real genetic spiral, becoming visible in this way; but this is wholly impossible as according to all we know about phyllotaxis the stamens placed before the sepals 1, 2, 3, 4, 5 are not the numbers 11, 12, 13, 14, 15 but 14, 15, 11, 12, 13.

Here the only explanation must be that the stamens, though having been laid down in a spiral order themselves and having become simultaneous in their appearance by the levelling of the whorl-forming factors, have been influenced by the subtending sepals in such a way that the existing differences in the developmental stages of the sepals have been transferred to the stamens.

Of course it would be easy to make detailed suppositions about the way in which this may be brought about, suppositions in which the achievement of the conducting tracts might play a rôle, but I shall leave this until more facts are known.

Finally in F, *Agrostemma Githago* we have an instance in which the same phenomenon is observed twice; the episepalous stamen whorl sheds first, in the order of the subtending sepals, the epipetalous whorl sheds in the order of the subtending petals, so that according to their genetic spiral the dehiscence order becomes: 19, 20, 16, 17, 18.

Even for those who are not disposed to go so far as to assume a spiral origin for the stamens, the real existence of the one-sided and the local influences on the stamens is not to be denied. And once this is granted there is no reason to deny the possibility of the existence of analogous influences acting on the petals.

The second point for our general discussion was the question as to how far the facts furnish real evidence for the spiral origin of the corolla.

In several cases we met with corolla edges in which the overlapping of the petals was such as might have been expected from differences in height of insertion according to the assumed spiral; the overlapping was eutopic. Yet in other cases we found corolla edges which were decidedly metatopic in the great majority of cases. For the explanation of these metatopies the "local influences" discussed above were assumed; it is however clear that the cogency of the argument derived from the eutopic cases is weakened in this way, and the question has to be put whether any conclusive power may be left.

The question has been discussed already for the zygomorphic flowers in Chapter 6, where I came to the conclusion that in zygomorphic flowers, though the cogency of the arguments had been diminished, yet the facts were still in favour of the spiral origin.

In the variably imbricate corollas the same was decidedly the case. But perhaps the best evidence is furnished by the heterotropic contort

corolla. For here we meet with several cases in which the "rational faults" prevail over the "irrational", and even in one case, in the second flowers of *Goniolimon tataricum*, we have a condition in which, the contortion disappearing altogether, a variable imbrication with a strong tendency to eutopy is left.

Stronger even than these facts is the circumstance that the assumption of a spiral origin of the corolla allows of a rational explanation of the curious relation between calyx spiral and corolla contortion in the heterotropic corolla, and moreover of the fact that this relation is reversed for the heterotropic calyx.

In the light of this explanation it is perhaps no casualty that in the heterotropic corolla the remains of the original spiral in the form of eutopic overlappings are more frequent than elsewhere; if the explanation holds true, the heterotropic aestivation is only possible in a corolla where the original spiral has not been lost completely at a somewhat advanced stage of the development.

So my conclusion is, that notwithstanding the many biasing factors the evidence from the corolla aestivation is distinctly favourable for the assumption of the spiral origin which is urged too by so many other facts.

Unless facts pointing to the contrary are brought forward, we may therefore assume that the corolla is laid down in Dicotyledons in a spiral order, but that the whorl-forming factors are so strong, that in most cases hardly any or no traces of the spiral are left, not even at that moment to which so great value is attached by many botanists, the first moment of appearance of the primordia.

This spiral order may be called a quincuncial one for the pentamerous flower, when we do not take the word in the narrow sense of a 144° divergence, but in the sense of a divergence of the main series, adapted more or less by metatopy to the requirements of the false whorled condition.

SUMMARY.

1. It has been tried to explain the intermediate conditions between spiral and whorled phyllotaxis in most Dicotyledonous flowers as false whorls, formed by special whorl-forming factors out of spirally laid down phyllomes.

2. The different views in literature on floral phyllotaxis are reviewed. Against the morphologists of the old school who mostly believed that all floral whorls are transformed parts of a spiral the later morphologists of rationalistic schools entertained different opinions about floral whorls in which the symmetry principle or similar ideas mostly play a prominent rôle.

3. The principal facts about corolla aestivation described in literature are reproduced: it appears that after a fruitful period in the times of BRAUN, WICHURA and WYDLER our knowledge of the facts has been hardly increased.

4. The principal modes of aestivation are described and a set of technical terms is chosen.

5. Starting from the supposition that floral whorls are transformed parts of a spiral it is discussed where remnants of this spiral are to be expected and how they may be recognized; methods are indicated for the investigation on this score of variably imbricate, zygomorphic and contort corollas. The methods being of a statistical kind, the theory of probabilities takes a prominent place in them.

6. For the elaboration of the method for the zygomorphic corolla suppositions are worked out about the essential qualities of the zygomorphic shoot; the relation between the symmetry plane and phyllotaxis is described.

7. For the elaboration of the method for the contort corolla suppositions are given on the nature of the contort corolla which are based on the facts of the distribution of the phenomena in the class of the Dicotyledons and upon the parallel between contortion and leaf twisting, drawn by WICHURA.

8. An explanation for the constant relation between calyx spiral and contortion direction in the heterotropic corolla is given which is based

on the spiral origin of the corolla and on the junction of the petals to the sepals; the fact that in the heterotropic calyx the relation is the reverse one is explained from the same premises, and the possibility is pointed out of an explanation on similar lines for the heterotropic contortion of the *Euphorbia* appendages.

9. Seventeen species with variably imbricate corollas are investigated, the conclusion being that in some of them the tendency to eutopy regularly prevails at all edges, in others at some edges only. The remaining edges may have either a chance distribution of the overlapping, or they may have a preponderance of metatopies for which fact special one-sided or local influences are claimed to be responsible.

10. Sixteen species with zygomorphic corolla aestivation are investigated, the conclusion being that outside the symmetry plane the aestivation is determined with more or less constancy by the zygomorphy factors and in the symmetry plane in several cases by the original spiral differences, in other cases by chance only; whereas in a few cases the overlapping in the symmetry plane becomes metatopical for which fact again special influences are claimed.

11. Ten species with contort corolla aestivation are examined. In the two species with autotropic corollas the deviations from contortion were determined by chance; in some species with heterotropic aestivation this was also the case, but in others there was a certain tendency to eutopy as the "rational faults", i.e. the eutopic deviations from contortion, prevailed over the "irrational faults", i.e. the metatopic deviations.

12. The phenomena of the anther dehiscence order as described by WYDLER are compared to those of the corolla aestivation and they are brought forward as an argument for the reality of the assumed special influences.

13. From all the related facts the conclusion is drawn that the Dicotyledonous corolla probably is laid down in the same spiral order as the calyx.

> *Botanical Laboratory of the Government University.*
Groningen, Sept. 1934.

LITERATURE.

1. AL. BRAUN, Vergl. Unters. ü. d. Ordnung der Schuppen an den Tannenzapfen etc., Nova Acta A.C.L.C.N.C. **15**, l. 1831, p. 196.
2. AL. BRAUN, Ueber die gesetzlichen Drehungen im Pflanzenreiche, besonders diejenigen, welche an Blüthen und Früchten vorkommen, Flora **22**, 1839, p. 311.
3. AL. BRAUN, Beitrag zur Feststellung natürlicher Gattungen unter den Sileneen, Flora **26**, 1843, p. 349.
4. AL. BRAUN, Ueber den Blüthenbau der Gattung Delphinium, Jahrb. f. wiss. Bot. **1**, 1858, p. 307.
5. L. et A. BRAVAIS, Essai sur la disposition des feuilles curvisériées, Ann. d. Sc. nat. 2e Sér. Bot. **7**, 1837, p. 42.
6. L. et A. BRAVAIS, Essai sur la disposition symétrique des inflorescences, ibid. p. 193 and **8**, 1837, p. 11.
7. L. et A. BRAVAIS, Essai sur la disposition générale des feuilles rectisériées, ibid, **12**, 1839, p. 5.
8. ADOLPHE BRONGNIART, Sur l'insertion relative des diverses pièces de chaque verticille floral, et sur son influence sur la régularité ou l'irrégularité des fleurs. Ann. d. Sc. nat. **23**, 1831, p. 225.
9. M. BREINDL, Zur Kenntnis der Baumechanik des Blütenkelches der Dikotylen, Botan. Archiv **36**, 1934, p. 191.
10. BULLIARD, Dictionnaire élémentaire de botanique, revu et presqu'entièrement refondu par Louis-Claude Richard, Paris An VIII—1800.
11. A. P. DE CANDOLLE, Théorie élémentaire de la Botanique, etc., Paris 1813.
12. A. P. DE CANDOLLE, Organographie végétale, etc., I, Paris 1827.
13. A. CHATIN, Mémoire sur la famille des Tropéolées, Ann. d. Sc. Nat. 4e Sér. Bot. **5**, 1856, p. 283.
14. L. J. CELAKOVSKÝ, Ueber den phylogenetischen Entwicklungsgang der Blüthe und über den Ursprung der Blumenkrone, Sitz. ber. d. kgl. böhm. Ges. d. Wiss. Math.-naturw. Cl. **40**, 1896, p. 1.
15. A. H. CHURCH, On the relation of phyllotaxis to mechanical laws, London, 1904.
16. A. H. CHURCH, Types of floral mechanism, I, Oxford 1908.
17. A. W. EICHLER, Blüthendiagramme, Leipzig 1875—1878.
18. K. GOEBEL, Organographie der Pflanzen, etc. Jena 1898—1901.
19. K. GOEBEL, Ueber Symmetrieverhältnisse in Blüten, Wiesner-Festschrift, Wien 1908, p. 151.
20. K. GOEBEL, Morphologische und biologische Bemerkungen, 21, Scheinwirtel, Flora **105**, 1912, p. 71.
21. K. GOEBEL, Organographie der Pflanzen, etc., 2nd ed, Jena 1913—1923.
22. ASA GRAY, Aestivation and its terminology, Amer. Jour. of Sc. and Arts. 3rd Ser. **10**, 1875, p. 339.
23. G. HENSLOW, On the origin of floral aestivations. With notes on the structure of the Cruciferous flower, on that of Adoxa and on the corolla of Primula, Trans. Linn. Soc. London 2nd Ser, Botany 1, 1880, p. 177.
24. A. DE SAINT HILAIRE, Leçons de Botanique, Paris 1841.
25. M. HIRMER, Zur Kenntnis der Schraubenstellungen im Pflanzenreich, Planta **14**, 1931, p. 132.
26. W. HOFMEISTER, Allgemeine Morphologie der Gewächse, Leipzig 1868.

27. TH. IRMISCH, Ueber die Knospenlage der Blumenkronblätter von Euphrasia lutea und von mehrern anderen verwandten Pflanzengattungen, Bot. Ztg. **5**, 1847, col. 81.
28. TH. IRMISCH, Ueber einige gamopetale Blüthen, Ibid. col. 641.
29. G. VAN ITERSON JR., Links en rechts in de levende natuur, Handel. v. h. 23e Ned. Nat. en Gen. Congr. te Delft 1931, Haarlem 1931, p. 4.
30. CH. KUNTH, Notice sur la vie et les travaux de Louis-Claude-Marie Richard, Ann. d. Sc. nat. **1**, 1824, p. 201.
31. H. J. LAM, Beiträge zur Morphologie der dreizähligen Burseraceae-Canarieae, Ann. de Buitenzorg **42**, 1931, p. 23.
32. C. F. PH. VON MARTIUS, Ueber die Architektonik der Blüthen, Isis oder encyclopädische Zeitung von Oken **21**, 1828, col. 522.
33. C. METTENIUS, Alexander Braun's Leben nach seinem handschriftlichen Nachlass dargestellt, Berlin 1882.
34. F. PAX, Allgemeine Morphologie der Pflanzen mit besonderer Berücksichtigung der Blüthenmorphologie, Stuttgart 1890.
35. J. B. PAYER, Traité d'organogénie comparée de la fleur, Paris 1857.
36. J. REINSCH, Ueber die Entstehung der Aestivationsformen von Kelch und Blumenkrone dikotyler Pflanzen und über die Beziehungen der Deckungsweisen zur Gesamtsymmetrie der Blüte, Flora **121**, 1927, p. 77.
37. W. ROBIJNS, L'organisation florale des Solanacées zygomorphes, Mém. Acad. roy. d. Belgique Cl. d. Sc **11**, 1931.
38. P. ROHRBACH, Ueber den Blüthenbau von Tropaeolum, Bot. Ztg. **27**, 1869, col. 833.
39. J. ROEPER, Normales und Abnormes, Bot. Ztg. **10**, 1852, col. 425.
40. K. FR. SCHIMPER, Beschreibung des Symphytum Zeyheri etc., Geigers Magazin f. Pharmacie **28**, 1829 (Quotations from the reprint Heidelberg 1835).
41. TH. SCHMUCKER, Rechts- und Linkstendenz bei Pflanzen, Beih. z. bot. Centr. **41**, 1924, Abt. I, p. 51.
42. K. SCHÖFFEL, Untersuchungen über den Blütenbau der Ranunculaceen, Planta **17**, 1932, p. 315.
43. J. C. SCHOUTE, Die Fehlerwahrscheinlichkeitstheorie für die Praxis der Versuchsstationen, Die Landwirtsch. Versuchsst. **70**, 1909, p. 161.
44. J. C. SCHOUTE, On whorled phyllotaxis, I, Growth whorls, Rec. trav. bot. néerl. **19**, 1922, p. 184.
45. J. C. SCHOUTE, On whorled phyllotaxis II, Late binding whorls of Peperomia, Ibid **22**, 1925, p. 128.
46. J. C. SCHOUTE, On the contort corolla, Proc. Kon. Akad. v. Wet. Amsterdam **34**, 1931, p. 1077.
47. J. C. SCHOUTE, Ueber die Caryophyllaceen-Dekussation, Ber. d. D. bot. Ges. **50**, 1932, p. 229.
48. J. C. SCHOUTE, Zur Erinnerung an Heinrich Wydler, Rec. trav. bot. néerl. **31**, 1934, p. 1.
49. J. C. SCHOUTE, Observations on the inflorescence in the family of the Plumbaginaceae, Ibid **32**, 1935.
50. J. C. SCHOUTE, Note on some properties of decussate foliage leaves which are connected with space-filling in the bud, Ibid. **32**, 1935.
51. K. SCHUMANN, Die Aestivation der Blüthen und ihre mechanischen Ursachen, Berichte d. D. bot. Ges., **4**, 1886, p. 53.
52. AD. STEINHEIL, Observations sur la tige du Lamium album, suivis de quelques réflexions sur l'estivation quinconciale, Ann. d. Sc. nat. 2e Sér. Bot., **1**, 1834, p. 87.
53. AD. STEINHEIL, Quelques observations relatives à la théorie de la phyllotaxis et des verticilles, Ibid, **4**, 1835, p. 100.
54. J. TROCHAIN, Etude morphologique et anatomique d'un Rhinopteryx (Malpighiacées) peu connu de l'Ouest africain, Bull. Soc. bot. d. Fr. **69**, 1932, p. 837.

55. W. TROLL, Organisation und Gestalt im Bereich der Blüte, Berlin, 1928.
56. R. VON VEH, Untersuchungen und Betrachtungen zum Blattstellungsproblem, Flora **125**, 1931, p. 83.
57. J. VELENOVSKY, Vergleichende Morphologie der Pflanzen, Prag 1905—1913.
58. R. WAGNER, Präflorationsformeln, Anz. Akad. d. Wiss. Wien math. nat. Kl. 1928, p. 156.
59. A. WEISSE, Die Zahl der Randblüthen an Compositenköpfchen in ihrer Beziehung zur Blattstellung und Ernährung, Jahrb. f. wiss. Bot: **30**, 1897, p. 453.
60. M. WICHURA, Ueber das Winden der Blätter, Flora **35**, 1852, p. 33.
61. H. WYDLER, Morphologische Mitteilungen, Bot. Ztg. **2**, 1844, col. 609.
62. H. WYDLER, Die Knospenlage der Blätter in übersichtlicher Zusammenstellung, Mitt. d. Berner Naturf. Ges. 1850, p. 145, and with some additions in Flora **34**, 1851, p. 113. (Quotations from Flora).
63. H. WYDLER, Fragmente zur Kenntniss der Verstäubungsfolge der Antheren, Flora **34**, 1851, p. 241.
64. H. WYDLER, Ueber die symmetrische Verzweigungsweise dichotomer Inflorescenzen, Ibid., p. 289.
65. H. WYDLER, Morphologische Notizen, Flora **39**, 1856, p. 33.
66. H. WYDLER, Morphologische Notizen, Flora **40**, 1857, p. 1.
67. H. WYDLER, Kleinere Beiträge zur Kenntniss einheimischer Gewächse, Flora **42**, 1859, p. 257.
68. H. WYDLER, Zur Morphologie, hauptsächlich der dichotomen Blüthenstände, Jahrb. f. wiss. Bot. **11**, 1878, p. 313.
69. A. ZAMELIS, Zum Blütenbau von Pirola uniflora L. nebst einigen allgemeinen Bemerkungen über die Knospendeckung aktinomorpher Blüten, Acta Horti Bot. Univ. Latviensis **3**, 1928, p. 219.