ON PLEIOMERY AND MEIOMERY IN THE FLOWER [1]

by

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§ 1. Introduction.

Every botanist knows that in most species of flowering plants the number of floral parts is not absolutely fixed, but that meristic variations may nearly always be found. Velenovský (24, p. 871) gives a series of five diagrams of terminal flowers in *Sanguisorba officinalis*, which are from trimerous up to heptamerous in their perianth and androecium.

This meristic variation is subject to certain general rules, which may be formulated as follows.

1. Generally speaking high numbers vary more than low ones; this has been pointed out already by A. P. de Candolle in 1813 (3, p. 134). Monocotyledons therefore vary less than Dicotyledons; on the whole the variation of Monocotyledons lies between 2 and 5, (cf. Eichler, 7, I, p. 152, *Roxburghia*, p. 150, *Paris*) and seldom goes higher [2]), whereas Dicotyledons range from 2 to 30 (cf. Eichler, 7, II, p. 56, *Dorstenia* and p. 418, *Sempervivum*).

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[1]) Extended form of paper read before Section M of the Fifth Botanical Congress at Cambridge, 1930.

[2]) The genus *Paris*, according to P. Stark (23, p. 287) ranges in some species viz *P. Franchetiana*, *P. japonica*, P. *Marchandii* and *P. yunnannensis* up to 7, 8, 9 or 10 in every floral whorl.

2. Some families are remarkably constant in their floral numbers, whereas others vary more readily. As very constant Eichler cites, (I, p. 10) *Umbelliferae, Cruciferae, Compositae,* and as often varying *Smilaceae, Cyperaceae, Primulaceae, Ericaceae, Jasmineae, Rutaceae, Rosaceae, Crassulaceae.*

3. Nutrition has a strongly marked influence on the variation, vigorous plants having a tendency to high numbers in their flowers, to pleiomery as it is called by Murbeck (14, p. 4), weak plants to low numbers, i.e. to meiomery; in many inflorescences the first formed flowers may be pleiomerous, the last ones meiomerous. In support of these facts I might quote a long list of examples from the literature; I shall confine myself however to one quotation, from Hugo de Vries, who concludes the section „Ernährung und Zuchtwahl" in his Mutationstheorie with the words: „Die fluktuirende Variabilität ist also eine Erscheinung der Ernährungsphysiologie" (25, p. 411).

4. In a number of cases the meristic variation in the flower is complicated by the occurrence of intermediate stages, in the form of connate or bilobed organs.

The rules here enumerated are not very surprising. Indeed, we may say that the first three rules seem to be inherent to meristic variation, that they are always to be observed whereever this kind of variability is found in living organisms; only the last rule as to the intermediate stages may sometimes fail, though it holds in many organisms with varying numbers of organs.

We might therefore expect that botanists would have taken such variations simply as a new example of the influence of nutrition on the plant body, without any further explication.

This is however not the case. The investigators have been induced, apparently by the associated features in flowers exhibiting variation, to adopt different conceptions about the causes of meristic variation, and so we find in the literature several views and explanations of the facts. As far as I know, it is only Eichler who throughout holds the opinion that a larger or smaller number of parts is simply due to what he calls original variation („originäre Variabilität, 7, I, p. 11); his view, however simple and natural it may be, has not been accepted by other botanists.

The different explanations of the authors may be divided into four groups.

Most morphologists try in some way or other to derive the abnormal numbers from the normal ones by peculiar morphogenetic processes; fission, dedoublement being responsible for the higher, fusion, connation for the lower numbers.

Another view is that higher numbers are due to the intercalation of new phyllomes between the existing ones, and the lower numbers to abortion of floral parts.

A third view is that it is not the phyllomes, but the floral receptacle which is responsible for the variation: the intercalation of a new sectorial region gives rise to supplementary organs, the omission of a sector in the construction of the receptacle is the cause of meiomery.

Finally a fourth view is that pleiomerous flowers are the result of the coalescence of two or more flowers.

The aim of this paper is to investigate the merits of these different conceptions; to make out, if possible, whether one and the same explanation should be accepted for all cases, and which of them should be accepted.

It is of course to the facts that we must have recourse as the only criteria; many facts will be found in literature, others I shall cite from my own observations on *Polygonum* and on *Lythrum Salicaria*.

The following seven paragraphs will therefore consider the five different conceptions and my own observations on the two mentioned objects, after which a concluding paragraph will summarise the results.

Though it is perhaps superfluous, I may remark that the meaning of the different terms, used to designate peculiarities of floral numbers, is the following. Pleiomery and meiomery are, as mentioned above, the presence of an unusually high or low floral number; iso- and heteromery denote flowers with either the same number in all whorls of the same flower, or with different numbers in the whorls of one flower; further in heteromerous flowers a whorl with more members than the others is polymerous, a whorl with lower number oligomerous.

§ 2. The fission and fusion theories.

The idea that fission and fusion are the causes of meristic variation is very wide-spread in the literature; indeed it turns up every now and then incidentally, often on a very small basis of facts and without any reference to previous work on the subject. For many authors the simple fact that a flower is hexamerous instead of pentamerous, is sufficient to prove that the underlying cause is a fission. It is only in a few cases that the author tries to get at a clear and definite conception as to the way in which the supposed morphological processes might take place, and it is evident that in these cases we may have two main points of view: the processes may be supposed to be either of a phylogenetic or an ontogenetic character.

The first point of view is fully elaborated by **Čelakovský**; the latter is taken by **Murbeck**. I shall therefore discuss the arguments of these two authors, ignoring the bulk of often indetermined and intermediate opinions.

Čelakovský has treated this subject in his paper on the reduction law of flowers (4); his idea is that a bilobed organ is not to be explained by the assumption of the fisssion of a simple one, nor by the fusion of two different organs; it is the outcome of two different tendencies, one towards forming a whorl with the lower, the other towards realizing the whorl with the higher number. From their combined action the intermediate form is the result. Čelakovský calls this process dedoublement, and distinguishes between positive and negative dedoublement. Positive dedoublement is the case where the tendency towards realizing the lower number is the original one, the tendency towards the higher number being phylogenetically younger; the reverse case is negative dedoublement. Both processes equally act on the number of members in a whorl as on the number of whorls itself.

As in Angiosperms the general tendency obviously is towards a fall in floral numbers, both in the cycles and in the members of the different zones, negative dedoublement must be the normal case. Positive dedoublement is only acknowledged by him in teratological cases, or in those organs which are reduced to trichomes or emergentia, like the pappus of many *Compositae.* (4, p. 135).

Čelakovský's idea of an inherited construction scheme is paralleled by many other similar biological conceptions, and surely is worth considering. The elaboration of any member of the plant must be the result of the interaction of several morphogenetic forces; these forces together may be called an inherited construction scheme of the member.

Yet in the given case certain objections may arise. We have to suppose that not only several morphogenetic forces are inherited, for which different genes may be responsible, but the number itself, e. g. five, also makes part of the inherited scheme.

When we ask how a number may be inherited, we might of course, as usually is done in phyllotaxis, consider it as the bulk relation of axis and primordia being such as to bring about a pentamerous whorl. This however is not Čelakovský's idea; apparently the number is for him a more direct part of the construction scheme, in a way that is difficult to grasp.

Now, whether we consider the laws of phyllotaxis as sufficiently cleared up or not, most morphologists agree that we must try to explain the phyllotactical relations from the concatenation of phyllomes according to the law of Hofmeister, and that the supposition of inherited construction schemes for phyllotactical systems should be avoided as long as possible.

There is however more to be said against Čelakovský's view. He himself rightly points to the analogous cases of bilobed foliage leaves. As in flowers, bilobed organs are often found between heteromerous whorls on one and the same stem, and the phenomena are so similar, that the explanation must be the same. It is therefore logically consistent, when Čelakovský (4, p. 6) applies the same explanation in the case of a plant with decussate leaves, which incidentally produces trimerous or tetramerous whorls, and in some whorls has a bilobed leaf.

But here we may remark, that bilobed leaves are not only found in transitions between whorls, but that they are equally frequent in most cases of irregular phyllotaxis, e. g. in fasciated stems. (6, p. 201). In such cases it is very difficult to use the same explanation, as there are no heteromerous whorls at all, but only a confused mass without any apparent construction scheme.

In a previous paper (19, p. 242) I have tried to demonstrate that the explanation of the bilobed leaves can only be given on the basis of the assumption that the growth processes of every leaf begin from a certain centre; when two of these centres arise nearer to each other than usual, the two leaves will meet in their expansion and may grow up with a common base, after having formed separate apices.

This explanation still seems to me the only one that explains the origin of bilobed organs, in irregular phyllotaxis as well as in whorls. Surely it is remarkable that both in the vegetative and in the reproductive part of the plant similar bilobed organs occur, whenever the conditions are such that some leaves may arise unusually closely together; in regular spiral foliar shoots they are not to be observed any more than in acyclic flowers.

The conception of Čelakovský, which already has the disadvantage that it elucidates unexplained facts by the assumption of almost inconceivable properties of the protoplasm, here fails entirely; there is therefore no reason to maintain it for the flower.

I now come to Murbeck's point of view. Already the title of his paper: „Über die Baumechanik bei Änderungen im Zahlenverhältnis der Blüte" (14) gives an indication of the tendency of his work: Murbeck tries to determine the construction mechanics of the changes in floral numbers. At least this is what he pretends; the paper itself only contains a detailed description of a great number of adult flowers, with statistical data about the different cases. The knowledge of the mechanics is therefore to be derived from the observed transition series: anyone expecting to find measurements of forces or indications of the resolution of forces will be disappointed.

That meristic variation is not a phylogenetic, but an ontogenetic process is nowhere mentioned in the paper; yet I believe that it should be taken in that way. At least I cannot see how a phylogenetic „Baumechanik" might be conceivable.

In contrast with Čelakovský, Murbeck only treats the changes in a whorl, not the changes in the number of whorls. As this last variation is not the subject of the present paper, this point is of no importance here.

Notwithstanding the above remarks, Murbeck's paper is a most valuable contribution to our knowledge by the detailed and accurate observation of facts. I shall discuss these facts and their bearing on the problem in hand in the following six categories.

1. Murbeck states, that in the plants he examined, viz *Comarum palustre* and *Alchemilla vulgaris*, the transition series from a single floral member through a bilobed organ to two separate members, is complete and continuous. This result, which is in harmony with analogous results of previous authors in other plants, may be explained in several ways. Murbeck's view, that high numbers are caused by fission, low numbers by fusion, is therefore not yet established in this way.

2. If a transition series is taken as a real process, a gradual movement, the „new" members in it do not arise apart from others, but as individualized fractions of existing members; on the other hand members do not „disappear" without fusing with other members.

The same remark may be made here as about the first category.

3. The abnormalities in a flower are not distributed at random, but if there are several of them in the same flower, these are strictly localized on a radius of the flower in a serried group.

This statement is surely of general validity as long as we consider the completed changes: the pleiomerous and the meiomerous flowers are as regular as the normal ones. As soon however as we consider the intermediate stages, the statement becomes too dogmatic. A tendency for more abnormalities to occur on one and the same radius is not to be denied, but on the other hand many cases are to be noted of flowers with two abnormalities on different sides of the flower; I shall return to this in § 8 on *Lythrum*.

Putting this detail aside, there remains a strong tendency towards sectorial variation. According to Murbeck this is due to the fact (14, p. 35) that the main vascular bundles, supplying the floral sectors, may either split or fuse, which in its turn similarly affects the members in these sectors. In this way indeed a rational explanation of the sectorial variation would be attained.

In an earlier paper (20, p. 156) I gave fresh arguments for the thesis, already proved by von Nägeli, that leaf traces are not formed in acropetal, but in basipetal direction; if this holds good, the explanation of Murbeck cannot be right. In my account of *Lythrum* this doubt will be fully confirmed.

4. The transition series between a single and a doubled member does not follow a well defined path: on the contrary the intermediate stages are of the most varying description.

The meaning of this new and important result will be best explained by an example. The addition of a new sepal in the flower of *Comarum* may arise, according to Murbeck's observations, by fission of another sepal. But it may equally well arise by the outgrow of a leaf of the epicalyx, or by fission of a petal and transmutation of one of the products into a sepal.

One would expect that if multiplication of floral parts took place in such a phantastic way, the pleiomerous flowers would constitute a chaotic conglomerate: but on the contrary, as we get nearer in the series to the next whole number, everything is rearranged as it ought to be according to the floral diagram, and the exceptional hexamerous flower is quite as regularly built as the normal pentamerous one. A fission on an episepalous radius moreover gives exactly the same result as a fission on an epipetalous radius; this strange result is not only obtained by Murbeck in *Comarum* and *Alchemilla,* but also by his pupil Lundblad in *Polygonum* (11, p. 10, 12, 26).

These facts, which are fully established by the numerous observations, are not very favourable to the fission and fusion hypothesis, and demand a better explanation of the forces governing the floral diagram.

5. Any transition series may be read in either direction; from the series itself it is impossible to tell, whether it leads from a single to a doubled member or from two organs towards a fusion product. The same fact has been observed by Stark in *Paris quadrifolia* (23, p. 277).

This fact, which fits in very well with the preceding category, would be very natural on the basis of original variation; for the fusion and fission conception it is an unexpected and curious phenomenon.

6. Pleiomery is more frequent on an episepalous radius than on an epipetalous one; meiomery on the other hand is more frequent on epipetalous radii.

This fact, which is not less remarkable than the two preceding ones, has been observed by Murbeck both in *Comarum* (14, p. 8, 19) and in *Alchemilla* (14, p. 26, 29). The observed frequencies are not given, yet there is no doubt as to the fact itself. We find it again in the observations of Stark on *Paris* (23). Stark gives a table 23 with the formulae of 12818 observed flowers. From this table we may gather that the calyx had one member more than the corolla in 565 flowers, one member less in only 32; the episepalous stamen whorl had one member more than the epipetalous one in 659, one stamen less in only 60 cases.

Murbeck tries to explain the facts as follows. Calyx veins generally are stronger than corolla veins; they will therefore form better conducting channels for nourishing substances. The organs placed on their radii will be better nourished and will more easily multiply; the less nourished epipetalous organs on the other hand will have a tendency towards diminishing numbers.

This method of explanation is again incorrect; the presence of the vascular bundles is determined by the foliar members and not reversely. Besides it is not established that calyx veins are stronger than corolla veins; my *Lythrum* material will show an example of apparent equality of the veins, and will yet give the same general rule as *Comarum*.

Stark, who like Murbeck starts from principles of construction mechanics, gives another and more obvious explanation, in considering space relations as the causes of the described phenomena. Whenever the leaf whorl in *Paris* becomes pentamerous instead of tetramerous, the available room in the flowers is increased so that fission is promoted, in outer whorls first, in inner whorls afterwards.

This explanation, which surely is much more satisfactory, will be discussed in § 6; we shall see there that the facts may be explained quite as well or even better on the basis of original variation.

So far we have considered the facts, observed by Murbeck. When we ask whether his arguments in favour of fission and fusion are sufficient to establish the view, that meristic variation is to be explained in this way, I feel obliged to deny the question completely. The facts are partly unfavourable, and those facts that might be used in favour are all open to other explanations.

A deliberatedly derogatory circumstance is further that Murbeck is obliged to suppose two different processes in the plant, fusion and fission, but is never able to discriminate between the two.

Murbeck takes the mean floral number as the starting point, and regards higher numbers as having originated by fission, lower by fusion. When a species with pentamerous flowers produces a flower with three normal sectors and two partly doubled ones, he is obliged to assume that one of these two sectors is in a fusing, the other in a splitting condition, but he is not able to tell which is which (14, p. 21, 31).

We might ask whether a normal number must be the starting point. What is a normal number? In my opinion this question is not to be solved satisfactorily; it opens a wide field of useless speculation. One might say: three is the normal number for Monocotyledons; and *Paris* is pleiomerous by fission. We might however just as well consider this generalization too wide and take as the normal number the number prevailing in the family, in the genus or in the species. The last evidently is Murbeck's choice. But we may then ask whether a constant variety with another floral number is not worthy to have a normal number of its own, and once this is granted, we may ask, whether *Adoxa* does not have two normal numbers, one for terminal and one for lateral flowers.

The whole difficulty disappears of course as soon as we drop one of the two supposed processes and derive every number either from the highest one by fusion, or from the lowest one by fission. This last idea is held by Velenovský (24, p. 870). But it implies that whenever a botanist is so unfortunate as to find a flower with a lower floral number than the lowest one on record for the species, he is obliged to change his idea of the fundamental number in the whole species, and the theoretical fissions in every whorl have to be raised by one. And the same remark might of course be made for the reverse assumption that everything was due to fusion.

Finally there still remains one objection against the fission and fusion conception, perhaps the most serious of all, in as far as that the morphological conceptions of real fission and fusion processes must be such as entirely to preclude their use in the explanation of pleiomery and meiomery.

Real fission surely occurs often enough in the flower; it is compared by **Eichler** with the occurrence of compound foliage leaves (7, I, p. 5), and doubtless this is right. **Velenovský** describes (24, p. 499) the interesting case of *Micrantheum ericoides*, with sessile trifoliolate leaves. The three leaflets and the two stipules are inserted on the stem as a row of five separate organs.

If we consider fission in this light, it becomes a well defined morphological phenomenon, a phenomenon that is also present in many flowers, especially in the androecium. When it occurs however, it is not confined to one single stamen, but is to be seen in all stamens of the same kind: in actinomorphic flowers in the whole whorl and in zygomorphic flowers in all stamens of the same differentiation.

We may be sure that peculiar morphogenetic forces act on such compound stamens, forces which are responsible for part of their plastics. The characteristic of meristic variation, as conceived by **Murbeck**, is that it works on a single sector, not on the other floral parts of the same differentiation; it is not conceivable how this can be compatible with the idea that the form of every part of the plant is due to certain definite morphogenetic forces.

Similar remarks may be made on fusion. The connation of floral parts is a very familiar phenomenon, but it is again not limited to one single pair of organs, if there are more of the same differentiation; unless the two are from the beginning nearer to each other than usual. The intermediate stages, with their bilobed organs, may therefore be explained quite well by fusion. But meiomerous flowers no longer show any fusion, they are simple provided with a lower number of organs than usual.

§ 3. Intercalation of new organs and abortion.

It seems to be a psychological fact, that when a flower is meiomerous, the idea of abortion of certain members presents itself as readily as that of fusion, whereas in the case of pleiomery it is only fission that seems obvious, and the reverse of abortion, the formation of new members, is not an idea which attracts.

Consequently though it may not seem quite logical, I have here to restrict myself to abortion as the cause of meiomery, and as an author who takes this view I may cite H. Gross. In his paper on *Polygonaceae,* Gross derives (10, p. 236) all pentamerous flowers of the family from the hexamerous flower of *Rumex* by abortion of one of the outer tepals; his chief argument being that the difference between cyclic and acyclic flowers is a fundamental one, without which taxonomy of the Angiosperms is impossible. The idea that one individual plant might have both kinds of flowers is an absurdity, and a *Polygonum* with pentamerous and hexamerous flowers only proves that both flowers are essentially the same. Gross therefore describes the pentamerous flower as cyclic, notwithstanding the apparent $^2/_5$ spiral in its perianth.

As the thesis of Gross is only founded on general considerations, not on special facts, it is only necessary to remark here that the difficulty of the occurrence of two kinds of flowers on a single plant may be equally well met by the reverse explanation, namely, that the hexamerous Polygonaceous flower as well as the pentamerous one is spiral: in doing so we have the great advantage that not only the harmony with the general considerations is maintained, but that we are also in accordance with many facts.

Of these facts I shall here only mention that Payer observed (15, p. 290) that in *Rheum* the outer tepals arise in a spiral order, a fact which has since been confirmed by Bauer (1, p. 287). There is therefore no reason whatever for the assumption of abortion in the perianth.

We might remark besides that abortion just as fission and fusion, is a real ontogenetic process, the extreme of retardation. In many flowers we have good evidence of abortion, e. g. in the outer stamen whorl of *Primula*, or in the fifth stamen of *Lamium*. This abortion in actinomorphic flowers influences whole whorls, not single members; that it will lead to meiomery is impossible in actinomorphic flowers, and in zygomorphic ones it may only bring about a pseudomeiomery, not a real one.

§ 4. The intercalation or omission of sectors in the floral receptacle.

The idea, that in the floral receptacle sectors may be intercalated or omitted, is due to Goebel. I have not been able to find the exact place where it is enounced for the first time, but we may find it, for example in the second edition of the Organographie. Fission as a means of multiplying floral members is recognized by Goebel in double flowers: a carnation with 48 petals owes this large number (9, p. 1579) to the development, in addition to the five normal petals, of ten petaloid divided stamen primordia.

His explanation of pleiomery and meiomery is however different. According to his view (9, p. 1582) „beruht jede Änderung in der Blattstellung auf einer Änderung in der Beschaffenheit des Vegetationspunktes. Ein Vegetationspunkt einer Pflanze mit dreizähligen Wirteln ist kräftiger, d. h. reicher mit Baumaterial ausgestattet, als der derselben Art mit zweizähligen Wirteln, eine Annahme, womit auch die Tatsache stimmt, dass die Vermehrung der Quirlblätter namentlich an gut ernährten, üppig wachsenden Pflanzen auftritt". So far we can fully agree: this is what Eichler means by his original variation. He continues however: „Wir können auch sagen, bei Pflanzen, welche von der Zwei- zur Dreizahl übergehen, werde am

Vegetationspunkt ein Sektor eingeschaltet. Tritt dies ein, zu der Zeit, in der schon junge Blattanlagen vorhanden sind, und fällt die (nicht sofort in vollem Masse eintretende) Sektoreneinschaltung bezw. Umfangsvergrösserung auf eine der beiden Blattanlagen, so wird — je nach dem Zeitpunkt — diese als mehr oder minder tief geteiltes Doppelblatt sich ausbilden".

Here we have the intercalation of a sector. We see that it implies that the enlargement of the vegetative cone might sometimes take place after the laying down of the leaf primordia. In my opinion this cannot be right: we have to suppose that the changes in bulk of the vegetative cone are previous to the formation of the primordia, and in any case we have to suppose that this enlargement is not sectorial but equal all round.

The conception of the bilobed organs is changed entirely by Goebel's outlook on the phenomena; he continues: „Die „zweispaltigen" Blätter erscheinen als ein nicht vollständig geglückter Versuch statt Eines Blattes deren zwei zu bilden. Wir legen also auf die bei diesem Vorgang eintretende „Teilung" der Blattanlage gar kein Gewicht. Denn ein solches Doppelblatt kann umgekehrt auch beim Übergang von einem dreizähligen Blattwirtel in einen zweizähligen auftreten. Dann aber liegt natürlich nicht eine Teilung, sondern ein zusammenrücken zweier Blattanlagen auf. Es tritt am Vegetationspunkt die Minderung eines Sektors und im Zusammenhang damit ein Zusammenrücken von Blattanlagen ein. Aber das eine wie das andere findet nur an den Übergangsstellen statt. Wenn die Änderung des Vegetationspunktes einmal vollzogen ist, treten an ihm die Blattanlagen — entsprechend der Regel der Äquidistanz — durchaus selbständig auf!"

We see that the description of the omission of a sector is also given here. The conception appears to be identical with that of the original variation of Eichler in the case of the whorls with whole numbers: the difference lies in the conception of the transition stages and the origin of these. The way in which the supposed intercalation and omission should be brought about, is by no means clear. Not only do we miss an attempt to work out the conception in more or less physiological terms, but such an attempt presumably would soon lead to the recognition of its impossibility.

Notwithstanding the vagueness of the conception, it has been used by other investigators. Murbeck in his paper fully treated above, has certain similar passages, in spite of his different point of view. The fact that several changes occur in a single sector makes him write that a group of organs „zwischen bereits vorhandene Gruppen eingeschoben oder ausgeschaltet wird" (14, p. 33) or as he expresses it elsewhere, that „die erforderlichen neuen Organe eine geschlossene Gruppe bilden, für welche dadurch Raum geschaffen wird, dass der Blütenboden sich an einer bestimmten Stelle seiner Peripherie gleichsam öffnet und zu einem neuen, sectorförmigen Teil erforderlicher Breite ausdehnt" (p. 8). This sentence, which reminds one more of the Arabian Nights than of a botanical paper, may be passed without discussion.

Bauer has used it further in his study on *Polygonaceae*. He quotes (1, p. 282) from Goebel the following further elaboration of the conception, from a place I was unable to find. The flower is a closed system with a definite quantity of nourishing substances. The distribution of these substances may be uniform, which condition gives rise to regular flowers; or the development of some sectors may be advanced and that of others kept back, which results in the flower becoming zygomorphic.

We see, that though Bauer's terminology is the same, the conception has entirely changed; it is no longer an intercalation, but a furtherance. Leaving this detail aside however, we may remark, that the difference between regular and zygomorphic flowers has nothing to do with the question of pleiomery and meiomery.

The observations of Bauer further give us another curious fact, which is difficult to explain by the intercalation and omission theory, either in Goebel's version or in Bauer's. If in a pentamerous Polygonaceous flower with a $^2/_5$ perianth, a sixth sector is to be intercalated, this nearly always takes place between the sepals 1 and 3 (1, p. 285, 286). According to the spiral theory of the flower, this is quite natural, as sepal 6 must lie there.

But if on the contrary a hexamerous *Rheum* loses a sector, it is exactly the same sector 6 between sepal 1 and 3 that disappears (p. 288).

This is a confirmation of the view that the apparently whorled hexamerous flower is really spiral. In the previous paragraph we saw that the outer whorl of perianth leaves in the *Polygonaceae* is formed in a spiral order. We here understand that the same order is continued in the inner whorl, as in the case of meiomery it is the highest tepal that no longer develops as such.

These facts imply on the other hand, that the intercalation and omission of sectors is controlled by the genetic spiral of the phyllomes. I believe that it might be difficult to get a better argument against the reality of intercalation and omission as processes in the floral receptacle.

Analogous results, partly more precisely elaborated, have been obtained by Lundblad (11, p. 8, 24, 38). In 123 flowers of *Polygonum Weyrichii* Lundblad found a fission in tepal 3 in 70 %, in tepals 4 and 5 in a total of 30 %, never in 1 or 2. This fission in 3 is the inclusion of the sixth phyllome in the perianth, fission in 4 and 5 is the inclusion of number 7 and 8, in 1 and 2 would be the inclusion of 9 or 10. Similar observations are recorded for *P. alpinum* and *P. baldschuanicum*.

We may conclude therefore that the theory, discussed in this paragraph meets with important objections, which are not balanced by any facts in favour of the conception.

§ 5. The coalescence hypothesis.

The idea that pleiomerous flowers are the products of the coalescence of two or more flowers was enounced in 1813 by A. P. de Candolle. After starting with the well known observations of double cherries, double strawberries etc. he remarks (3, p. 121) that connated flowers of *Labiatae* or *Personatae* rarely have a 10-lobed corolla and 8 stamens, but generally show lower numbers. He now supposes that all cases of „monstruosités par excès" may be explained in this way. He even goes so far as to explain the Cruciferous flower as formed from three collateral flowers, the two laterals being reduced to one single stamen.

It is not intended to deny that this explanation, curious as it may be, might do for pleiomerous flowers; for the equally important meiomerous flowers we should have to content ourselves with abortion. But it is perhaps hardly worth while to say that de Candolle's conception should only deserve consideration when there was reliable evidence in favour of it.

Just as two leaves may fuse when their centres lie too near to each other for the unimpeded development of each, so two buds may fuse in their earliest stages. In Delpino we find a detailed description (6, p. 209) of the behaviour of buds in the axil of doubled leaves. We learn that they may be double from the beginning and may consist when fully developed of a flattened stem, with a furrow on the upper and lower sides, the two parts of it separating higher up; it may begin however also as an apparently simple stem, which afterwards dichotomizes in a transverse plane.

Such cases, which I have frequently seen myself in *Helenium autumnale var. fasc.*, are very important for our theoretical conceptions of the nature of buds. In other cases the fusion is not lateral, but in the median plane, as in *Lonicera Alberti* (cf. Velenovský, 24, p. 822), where the terminal flower of the dichasium does not develop, and the lateral flowers expand in the earliest stages of their development until they meet and often fuse right over the vegetative cone of the parent axis, so as to form two connate flowers or even a single pleiomerous flower.

In such cases however we have sufficient means to determine the real condition, either from the phyllotaxis of the bracts, or from the construction of the flower itself; in § 8 I shall describe some such twin flowers of *Lythrum*.

But as in ordinary pleiomerous flowers the above morphological characteristics of doubleness are entirely absent, the coalescence hypothesis cannot give us the general explanation of the pleiomery of the flower.

§ 6. Original variation.

In the previous paragraphs we saw that the different views treated there, all met with more or less serious difficulties. We now have to consider original variation, the view held by Eichler, the greatest botanical morphologist of all time. I shall treat the four groups of facts in our introduction and the numerous facts described by Murbeck in the same order as above and discuss whether or not they give rise to objections to the view of original variation.

1. The fact that high numbers vary more than low ones, evidently fits in very well. When the number of a whorl depends upon the available room on a vegetative cone for leaf primordia of a given size, it is clear that in

the case of high numbers the chance of variation must be greater than in low numbers.

2. Some families are more constant in their floral numbers than others, even when the average numbers are the same. A direct explanation of such differences is surely not yet to be obtained from any of the theoretical conceptions; that these differences may exist however requires no more of original variation than the supposition that the relation in bulk of the young primordia to the floral receptacle is more constant in some families than in others at the moment of whorl formation. I cannot see any difficulty in that.

3. The strong influence of nutrition on floral numbers is paralleled by the phenomena in vegetative shoots of the plant, either with spiral or with whorled phyllotaxis. It is due to the simple fact that a better nourished and therefore larger vegetative cone has a larger surface and can bear more leaves.

4. The intermediate stages, fused or doubled or bilobed phyllomes as they may be called, are to be expected, as I have shown in a previous paper (19, p. 242), as soon as we assume that the development of any phyllome begins at a centre and gradually expands over the stem surface.

In some cases connation may easily take place, in others it is very rare. This may be due to the fact, that when two phyllomes are placed nearer to each other and therefore meet early in their development, each may cease to expand in the direction of its neighbour and the two may grow up close together but independently, or the two may grow together and produce a common basal part.

Thus in *Paris quadrifolia* we very seldom have bilobed organs in the foliage leaves and in the perianth (Stark, 23, p. 246), but more frequently in the androecium; in *Polygonum Weyrichii* they are common both in perianth and stamens (Lundblad 11, p. 8), in *Gentiana* spp.

they seem to be altogether absent in the flower, notwithstanding the frequent meristic variation (Geitler, 8, p. 239).

I now come to the numerous facts, observed by Murbeck, which I shall treat in the same order as above.

5. The completeness of the transition series between a single and a doubled member fits in with almost any conception of the nature of meristic variation, and is also in perfect harmony with original variation. As the two organs may arise at a smaller or greater distance, their united growth will begin earlier or later in their development.

6. Murbeck found that higher numbers were not the consequence of the addition of new members, but of fission, and reversely, lower numbers were not the consequence of abortion but of fusion. This conclusion, obtained from *Comarum* and *Alchemilla,* can be only valid in such cases where connation easily takes place. In cases where it is absent, the conditions must be different.

7. Furtheron we had the tendency towards the sectorial arrangement of abnormalities. Instead of inadequately explaining the facts by the intercalation of floral sectors or the splitting of vascular bundles, a much better explanation is to be reached on the basis of original variation in considering the conditions of false whorl formation.

If floral whorls are false whorls (cf. 22), the members are laid down in another phyllotaxis, mostly a spiral one. The young primordia are soon linked up by the whorl forming forces, and a certain metatopy is the outcome. The members usually soon become equidistant in the whorl by the simple fact that they are of about equal strength and expand until they meet each other. The successive whorls are adjusted to each other in a certain way; the common condition being that isomerous whorls become alternating, though in some cases they may become superposed. The way in which heteromerous whorls usually adjust themselves is described by **Eichler** (7, I, p. 11).

Now we must grant that the laws of false whorl formation itself, i.c. the rules by which the primordia are first linked up, are quite unknown: we only know that it must take place in such a way, that there is a strong tendency towards isomery, stronger perhaps than in binding whorls (21). But, whether these laws are known or not, we may be sure that in normal flowers, isomerous as well as heteromerous, the available room for every floral member will be such that the whole development up to the final stages can take place in due course. In flowers with abnormal numbers but with isomerous whorls, the same will be the case, as the excess or deficit of room will be balanced by the greater or smaller number of parts and will be evenly distributed over the flower; if however the abnormal flowers are heteromerous, the whorl numbers may be such as to cause difficulties as to space filling. If e. g. a flower has 5 sepals and 6 petals, it is evident that the adjustment processes described above must crowd two petals together. In such cases a bilobed petal may arise, namely if the petals have a tendency towards connation.

If such a process takes place in any whorl of an heteromerous flower, it is very probable that the higher whorls will be influenced, on the same radius, by the irregularity. For the simple fact of the strong tendency towards isomery of floral whorls sufficiently indicates that floral whorls in their first origin are partly determined by the lower existing ones. The tendency towards the sectorial arrangement of abnormalities may be very well explained in this way.

8. The strikingly varying character of intermediate stages between single and double members, and the curious way in which „new" members „originate" out of parts of quite different organs now becomes very

natural. After Murbeck's description we got the impression that in the intermediate stages all laws were suspended, only to come into force again as soon as the next whole number was approached.

The fact is however that in isomerous flowers every member has its own place for development, whereas in abnormal flowers some members may be crowded together; not only the members of a single whorl, but a member may be crowded out of the row and may fuse with a member of another whorl.

9. The fact that transition series may be read in either direction was a serious objection against the fission and fusion hypothesis. It is however a natural sequel to the views set forth above.

10. Lastly we had the curious fact that pleiomery is more frequent on episepalous radii, meiomery on epipetalous radii. We saw that Stark explained this by space relations on the vegetative cone, in connection with fission and fusion; more space inducing fission, less space fusion.

On the basis of original variation we may use the same explanation of available space, without any fission. As the vegetative cone of the flower is a limited stem, whorl formation has to deal with less and less space for every whorl. Organs of about equal strength may therefore easily form whorls of diminishing number: the oligomery of the gynoecium of so many natural families is the outcome of the same cause.

In calyx and corolla diminishing numbers like 6,5 or 5,4 or 4,3 are therefore more probable than increasing ones like 5,6 or 4,5 or 3,4. A supernumerary sepal consequently is more probable than a supernumerary petal. Six sepals and five petals, when adjusted as far as possible to alternation, will yield two adjoining sepals or a bilobed sepal. This is described by Murbeck as episepalous pleiomery, or epipetalous meiomery as the case may be;

and when he finds these two to be more frequent than the reverse cases which are the outcome of the formula 5,6, this is quite as might be expected.

The fact that the same remarkable distribution of frequencies also occurs in *Paris* (and as we will see in *Lythrum*) is a new indication of the correctness of the Eichlerian view.

The above are the facts, observed by Murbeck. Before concluding this paragraph I want to discuss two other groups of facts in their bearing on the original variation theory: the twin flowers of De Candolle and the meristic differences which sometimes are to be seen between lateral and terminal flowers of the same plant.

When two leaves are so near to each other on a vegetative cone that they may fuse, it is evident that their axillary bud areas will also come into close proximity. The phenomena of twin flowers can all now easily be explained when we suppose that such areas may also fuse, and at such early stages, that no phyllomes have as yet been formed by the areas.

It is clear that the fusion may be more or less complete; the result may therefore be either a single bud or a connate pair; the shoot developed from it may be cylindrical or flattened. As the vegetative cone in many cases will be more or less elliptical in section, the tendency towards dichotomy in a transverse plane is very natural.

Moquin-Tandon (13) laid great stress upon the fact that in connate flowers the calyx of one component always unites with the calyx of the other, etc.: „on peut constater que les diverses parties de deux verticilles donnés, appartenant à deux fleurs différentes, se cherchent, *se choisissent,* si je puis m'exprimer ainsi, de manière que l'union s'opère entre celles qui ont la même forme et la même position". „Cette tendance à l'union des parties homologues, reconnue depuis longtemps dans la tératologie animale, est assurément une des lois les plus admirables de la monstruosité." (p. 267).

The cause of this is obvious. The two buds, when more or less forming a unity, are subject to the same morphogenetic forces. As long as the vegetative cone of the two components still forms a coherent area, the change in morphogenetic forces causing the differentiation of the next category of floral organs, will appear in the whole of the area at the same time, so that the floral zone necessarily remains continuous all around.

De Candolle (3 p. 120) and Moquin-Tandon (13 p. 265) thought that coalescence was usually accompanied by abortion of such parts as should have been formed on the contact sides: „la cohérence entraine toujours avec elle une gêne, un arrêt de développement du côté où elle a lieu", writes Moquin-Tandon (p. 265). This is not right in my opinion; the successive whorls are as usual formed according to the available space. If the cone is still a unity, the twin flower will form concentric whorls; if the cone is bilobed, or expressed perhaps better, as the vegetative cone divides into two, the distal whorls will surround the separate centres. In this way flowers with two distinct, closed gynoecia within an elliptical common androecium may be explained. The assumption of abortion is however not necessary; all the phenomena may be described as original variation.

Our last point was the difference in floral number between lateral and terminal flowers. In many species such differences are unknown; in others they may be observed however, either with great regularity or in a certain percentage of the flowers. I do not need here to give many facts; cases like *Adoxa Moschatellina* where the lateral flower has a higher number or *Ruta graveolens* where the reverse is the case, are known to every botanist.

As far as I can see, there are two reasons why a terminal flower may have a different floral number from a lateral one. The first is, that the phyllotaxis of the leaves or bracts on the main axis may be continued in the terminal flower; this has, for example, been recognized by Eichler (7, I, p. 273) for *Adoxa* and for the peloria of *Labiatae*, by Schmidt (18, p. 348) for the *Berberidaceae*.

The other reason is that the bulk relation between the vegetative cone and the primordia may be different in both kinds of flowers. A pronounced, I might say an exaggerated example of this is given by the peloria of *Digitalis purpurea*. Here we have the phenomenon that the main axis, which usually only forms bracts and nothing else, sometimes suddenly changes and instead forms sepals, petals, stamens, and carpels in due sequence. If this occurs on the main axis of a strong plant, the floral number may be excessively high, up to 24 (Penzig, 16, p. 117). In many cases proliferation follows, as the vegetative cone is not yet exhausted by the four floral zones.

At the same time that the phyllomes of the main axis cease to differentiate as bracts, their axillary buds cease to develop as flowers. In many cases however, there are intermediate stages between lateral flowers and wholly aborted buds, in the form of very reduced lateral flowers, without prophylls or calyx, consisting simply of a corolla tube with two or even one lobe: dimerous or even monomerous flowers. These remarkable formations were described by Vrolik (26, p. 13) and have since been noted by several authors (cf. Penzig, 16).

We see therefore that *Digitalis* offers not only examples of excessive pleiomery but at the same time of excessive meiomery; both are to be explained by original variation alone. Many authors have considered the huge peloria as fused flowers (Von Schlechtendahl, 17, col. 581), as synanthy (e. g. Masters 12, p. 58), gamogemmie (Vuillemin 27, p. 201) or whatever they may call it;

Worsdell treats the case under the heading fasciation (28, II, p. 49) and speaks of the absorption of several of the uppermost flowers into the raceme, but all these explanations seem wrong to me; the only fact to consider is that the flowers are formed on axes of very different size and with very different phyllotaxis. Velenovský writes (24, p. 907) that the floral number of the peloria has a tendency towards n5. This might be an indication of a fusion of n pentamerous flowers. The statement is not however confirmed by any data, and the records we find in literature of observations on floral numbers (Vrolik, 26, Braun, 2, Conwentz, 5) distinctly point to quite other numbers. 13 is especially very frequent for the big peloria, 7 or 8 for the minor and 5 for the smallest ones. Braun explains the occurrence of 13 by the 5/13 phyllotaxis of the bracts; and without doubt this is right, and similarly 8 and 5 may be expected in a Fibonacci spiral of the bracts.

In the same way in a Labiate the decussation of the main axis often makes the terminal pelory tetramerous; there is no difference between this case and *Digitalis* but for the circumstance that in *Digitalis* the size of the main axis exceeds that of the lateral branches to an unusual degree.

Concluding this paragraph, we may state that the conception of original variation meets all requirements and explains the facts of meristic variation in a satisfactory way.

§ 6. The Polygonaceous flower.

During the years 1923 to 1925 a rather extensive collection of *Polygonaceae* was grown in the Groningen Hortus Botanicus. I made use of the opportunity to study the floral morphology of the family, in the hope that I might get more insight into the phyllotaxis of the flower.

Notwithstanding the rich material and my continued efforts, I finally had to bring my studies to a close without definite results, as I gradually came to understand, that there are in the Polygonaceous flower several processes affecting the number of organs, and mixed up in such a way that they could hardly, if at all be disentangled.

As the *Polygonaceae* have played an important role in the literature on pleiomery and meiomery, it is perhaps worth while to give here a brief account of the difficulties I met with and to discuss their bearing on the topic in hand.

Two of these processes influencing the floral number have been indicated already by Eichler: dedoublement of stamens and abortion of stamens. We may add as a third one connation of perianth leaves. A fourth difficulty, which does not affect the number but no less obscures the diagram, is the metatopy of stamens.

1. Dedoublement of stamens. The existence of fission in the stamens placed opposite tepal 1 and 2, in hexamerous flowers also opposite 3, is assumed by Payer (15, p. 291) and Eichler, denied by Bauer (1, p. 291) and, at least for the genus *Polygonum*, by Velenovský (24, p. 850). The evidence on which these opinions are based is partly ontogenetic (and not over-conclusive, as it is used pro by Payer and contra by Bauer), and partly derived from the conditions obtaining in the adult flower (Eichler) namely from the arrangement in contracted pairs.

That two stamens out of a whorl of three should be doubled, might seem improbable, in the light of the considerations of p. 176. In this peculiar case there is however no objection against the reality of the phenomenon on such grounds: the two stamens, being placed immediately opposite an outer tepal and at the margins of two inner petals, grow up under other conditions than the third one opposite the place where two inner tepals overlap. As soon as the perianth becomes hexamerous, and the conditions for the third stamen become the same as those for the other two, we see an analogous pair of stamens placed opposite tepal 3.

From my observations I shall cite the following facts which may be considered in connection with the question.

If there is a dedoublement, we may expect that this will in some cases fail to occur. This is what we actually see in many flowers. In *Polygonum aviculare* we may often see one single stamen opposite one of the first tepals; the distinction of subspecies even takes account of the number of stamens; the subspecies *heterophyllum* Lindman being characterized by 8, the subspecies *aequale* Lindman by 5 to 7 stamens. In my material, which had not been determined as to the subspecies, I observed out of 169 flowers, 99 with a single stamen immediately opposite tepal 1 and 97 with the same opposite tepal 2. In a few cases the single stamen had a broadened filament or bore 3 or 4 thecae.

In *Polygonum plebeium* pairs of stamens never occur opposite 1 and 2; in my material there were always either 5 or 6 epitepalous stamens, which might be numbered as 6—11; 6,7 and 9 being placed immediately opposite 1,2 and 4; 8 alternating with 3 and 5, and 10 and 11 obliquely opposite 5 and 3.

In the same way *Oxyria digyna*, which has a tetramerous perianth and normally six stamens, a pair opposite each of the outer tepals and a single stamen opposite the inner tepals, sometimes showed a single stamen corresponding with one of the outer tepals or with both of them.

In the second place we might expect that if dedoublement is one of the morphological processes occurring in the flower, it will be displayed in other stamens from time to time. In *Polygonum aviculare* I observed a pair of stamens instead of a single one: between tepal 3 and 5 twice; in the inner whorl of three stamens 19 times, viz 16 times opposite tepal 4 and 3 times opposite 5. In *Oxyria digyna* the single stamens opposite the inner tepals were in a few cases also replaced by a pair.

A third criterion we may examine is the following. If there is no dedoublement at all, the pairs of stamens opposite 1 and 2 in a pentamerous flower may be the numbers 6 and 9 and numbers 7 and 10; in a hexamerous flower the numbers may be 9, 12; 7, 10 and 8, 11. If this were the case a certain obliquity might perhaps in some instances be exhibited by the pair, owing to the fact that the component with the larger number was inserted somewhat higher, i. e more towards the interior of the flower. In spite of many observations, made especially for this purpose, I failed to note anything of that kind.

The above arguments advocating dedoublement are from my own observations. I might further add the following consideration.

If the Polygonaceous flower is originally spiral, the normal diagrams of the family as given by Eichler (7, II, p. 72), all show the spiral from the prophylls up to the carpels unbroken and in due order, at least when we consider the pairs as single numbers. The divergences in that case are all normal; for trimerous whorls we have the regular succession of two angles of 120° and one of 180°, for pentamerous cycles we have 144°, for dimerous cycles the regular succession of angles of 90° and 180°, as one would expect. The aborted stamens have to be taken into account.

If, on the contrary, we take every component of a pair as a separate phyllome, this is no longer true; in diagrams E, F, G, H and I the members no longer number according to such a spiral. In E for example we reach 10, but then we meet a divergence of either about 45° or about 200° and in the other diagrams the difficulties are of the same kind, whether we count the aborted stamens or not.

So far things seem to be reasonably clear. It is however a peculiarity of the family — at least such was my experience — that it first seems to yield certain results, which afterwards prove quite uncertain. We shall see that our arguments are more or less invalidated one by one, when we consider the next points of incertitude.

2. The abortion of stamens. Anyone examining many flowers of the family will be impressed by the fact that, though the number of stamens may vary to a considerable extent, the position of the pistil remains unchanged. Bauer writes „dass sich.... zwei Karpiden unter allen Umständen in die Richtung P_1—P_2 einzustellen suchen" (1, p. 279) and indeed it is striking that dimerous pistils always have their carpels opposite tepal 1 and 2 and that trimerous pistils have two of their carpels in the same position. Even if a species with trimerous pistils forms a dimerous one as a rare exception, this nearly always follows the same rule. The number of stamens may vary from 4 to 8, especially by the development of more or less inner stamens, but the pistil keeps its position, with very few exceptions.

I shall return to this pistil position afterwards; it is however clear that the fact itself points to a frequent abortion of stamens. In Eichler's diagrams F—I we find such aborted stamens represented by asterisks; in many abnormal cases these aborted stamens of the diagrams may develop again.

It is of course evident, that the common occurrence of abortion is a great impediment to the understanding of the floral construction.

Now things would still not be so bad if it were always the highest stamens in the spiral series that disappeared, so that a definite part of the spiral would be absent, whereas it would reappear in the pistil again. In some species this seems actually to be so. In *Polygonum aviculare* rather frequently one of the inner stamens is missing. If we number the stamens according to the dedoublement conception, the inner stamens are numbered 9, 10 and 11. Of these 9 was never absent in my material, 10 only once and 11 no less than 83 times in 150 flowers. If on the contrary, we number the inner stamens according to the idea that every component of a stamen is a separate phyllome, the numbers are 11, 12 and 13, and it is 11 that is often absent.

It seems therefore as if the abortion of stamens, instead of making the interpretation more difficult, provides us with an excellent means for discriminating between the dedoublement or non-dedoublement conception. But further observations soon undeceive the investigator: the *Polygonum* flower is not so easily explained.

Firstly *P. aviculare* itself. The pistil is normally trimerous. The three sides of the ovary may be of equal breadth, but very often one side is narrower than the other two. This narrow side invariably faces tepal 3. The style opposite 3 in such cases is often weaker, sometimes connate with one of the others. It seems as if this pistil is a transition towards the dimerous condition, which also rarely occurs in the species (2 in 170 flowers) and in which the carpels are opposite tepals 1 and 2.

In 17 cases a fourth carpel was present, sometimes as a small accessory rib and a small style; this was situated opposite tepal 4. In other cases the fourth carpel was as strongly developed as the others and then the four were equidistant.

In 5 cases finally a fifth carpel was to be seen, always opposite tepal 5; the five carpels then all being opposite to the tepals.

This series of observations leads to the assumption of a genetic spiral in the gynoecium in the same sense as in the other floral organs; this seems a strong point in support of the dedoublement theory. There is however one serious drawback: the spiral does not fit in with that of the stamens; between stamen 11 and the first carpel we have two empty places for the non existing numbers 12 and 13, as the first carpel stands in the position of 14. If there was no dedoublement, the stamens would number up to 13 and the two spirals would fit in with each other perfectly.

Now if we really would assume two empty places, it might be expected that stamens 12 and 13 would develop in some cases. Perhaps the dedoublement of „9" and „10", mentioned above may really have been a development of 12 and 13, which were shifted a little so as to form a pair with 9 and 10. But here we are again amidst the incertitudes and we have no means of getting clear of them. Thus our best example, *P. aviculare* leaves us with much doubt.

In other species with pentamerous flowers the presence or absence of the inner stamens was of much more irregular occurrence. I may cite the following observations.

Of the inner stamens missing:	„9"	„10"	„11"	
in *Polygonum capitatum*	1	8	4	times
P. filicaule	117	64	5	
P. minus	22	23	27	
P. molle	25	6	23	
P. tinctorium	0	15	21	

By „9" I mean the stamen opposite tepal 4, which gets the number 9 from the dedoublement conception.

Thus we see it is only *P. tinctorium* that here behaves in the same way as *P. aviculare*; three of the other species, *capitatum*, *minus* and *molle* show more or less a chance variation, whereas *filicaule* follows a distinct rule, the causes of which however remain in the dark.

3. Connation of perianth leaves. In many species the number of tepals is easily determined. In some cases there

may be some difficulty, viz when there are intermediate stages between tepals and stamens, but otherwise everything is straightforward. In other species there are indications of connation of tepals; this was very evident in *Polygonum Hydropiper*. Of 127 flowers of wild plants collected near Midsland (Texel) 115 were trimerous, 12 tetramerous in their perianth. It looked however as if all flowers in reality were pentamerous, with some fused tepals.

The tetramerous flowers had one very broad tepal, twice in the position where a normal pentamerous flower has its second and fourth tepal, ten times in place of 3 and 5. The position and number of stamens did not differ sensibly.

The trimerous flowers had two such connated pairs, one representing 2 and 4, one 3 and 5; in one case only was there an extremely broad tepal in place of 1, 4 and 2, more than half amplexicaul, and two normal ones in the position of 3 and 5.

In 22 cases the broad tepals were even bilobed, so that there can be little doubt as to the real occurrence of connation.

Similar results were obtained in *P. mite* and *P. minus*. In *P. mite* I observed out of 50 flowers, 5 with a pentamerous perianth, 27 with a tetramerous and 15 with a trimerous perianth. The tetramerous were, judged as seen by the eye, 14 with 1, 2 + 4, 3, 5; 12 with 1, 2, 3 +5, 4 and one with 1, 2 + 5, 3, 4. The trimerous cases were all 1, 2 + 4, 3 + 5. Bilobed tepals were not observed. In *P. minus* out of 104 flowers 95 had a pentamerous perianth, 8 a tetramerous, 1 a trimerous; these cases were all 1, 2 + 4, 3, 5 and 1, 2 + 4, 3 + 5. Several bilobed tepals were observed.

In both species the number and position of stamens were only little affected by the connation. It is clear however that the interpretation of the floral diagram is again much impeded by the possibility of complete connation.

4. Metatopy of stamens. The outer stamens in many species are placed immediately opposite the margins of the inner tepals. In two species with different breadth of tepals the position of the corresponding stamens is therefore not the same. The two stamens opposite tepal 1 or 2 are very close to each other when the inner tepals are broad, but wide apart when these are narrow. In *Polygonum amphibium* there are usually 5 stamens, two pairs opposite 1 and 2, one single stamen between 3 and 5. These 5 nearly form a regular pentagon, alternating with the tepals; on closer examination we see that the two components of a pair are somewhat nearer to each other than to the single stamen.

In *Polygonum mite* I observed another metatopy, not lateral, but in height. Usually there are 5 or 6 stamens; 5 in the outer whorl and sometimes 1 as the beginning of an inner whorl. In such cases, where tepal 2 and 4 are fused, the pair of stamens opposite 1 retains its position, but in that opposite 2 the component which should stand at the fused margin of 4 has been shifted towards the interior of the flower, like an inner stamen.

These observations, though in themselves of minor importance, tend to weaken the belief in the dedoublement of the outer stamens. For when the stamens may be easily shifted in connection with the position of the tepal margins, the pairs may just as well be separate stamens, crowded together by the margins of the inner tepals so as to form a pair.

Eichler's chief argument for the assumption of dedoublement therefore loses much of its pregnancy. Above I remarked that the same would be the fate of our other arguments; I trust that this will have become clear to the reader.

The argument that dedoublement sometimes seems to be absent may be refuted by the remark that the easy abortion and displacement of stamens may give the same result in appearance; that some stamens which usually are simple sometimes seem to have been doubled, may be explained by the development of inner stamens which usually abort. Similarly our argument assumed from the continuity of the genetic spiral in the flower brought us into difficulties as to the sequence of the carpels in *Polygonum aviculare*.

Our conclusion as to dedoublement therefore is, that it is not improbable, but that its existance is far from being established. The occurrence of connation of tepals and of abortion and metatopy of stamens seems to be beyond doubt, the existence of original variation on the other hand, though hardly to be denied on general considerations, is very difficult to demonstrate, as every individual case may be explained by the other processes. Real original variation would be established for example, when we can prove that the sixth phyllome of the flower differentiates as a stamen (or a pair of stamens) in the pentamerous, and as a tepal in the hexamerous flower. And though I suppose this to be the case, I have never felt quite sure of it, and I have certainly not been able to find an unquestionable proof.

Most authors have not fully recognized the difficulties mentioned above and consequently their conclusions are in many cases uncertain.

§ 8. Lythrum Salicaria.

Wild plants from the Elsburger Onland near Groningen were examined in the following way. Spikes of the three forms were picked: their expanded flowers were examined and the floral numbers were noted down, together with the position of the flower in the partial inflorescence.

As soon as a flower showed an abnormality other than meristic variation, its calyx was cut off just above the disc, it was opened by a longitudinal slit, the petals were removed after having being counted and the whole calyx with epicalyx and stamens mounted on a slide in glycerine.

This way of working was continued until 50 abnormal flowers of each of the three forms were gathered; 33 of each in 1928, the remainder in 1929.

In the first place I shall here give the floral numbers of the observed flowers. The partial inflorescence of *Lythrum Salicaria* is known to consist of a main flower in the axil of the bract, with two lateral prophylls, two lateral flowers in the axils of the prophylls and two accessory flowers developed from serially descending buds in the axils of the same prophylls, so that a transverse row of five flowers arises, and further, generally two similar, but somewhat weaker transverse rows from serially descending buds in the axil of the bract, opposite the main flower.

Lythrum Salicaria	Long-styled	Mid-styled	Short-styled	Total
Main flower	5.9 (93)	6.0 (112)	5.8 (39)	5.9 (519)
	6.0 (61)	5.9 (114)	5.8 (100)	
Lateral flower of main flower	5.1 (106)	5.1 (112)	4.9 (66)	5.1 (513)
	5.1 (82)	5.1 (76)	5.0 (71)	
Accessory flower of same	5.8 (22)	5.8 (25)	5.4 (21)	5.8 (117)
	5.9 (18)	5.8 (23)	5.1 (8)	
First access. flower of main flower .	5.7 (69)	5.8 (65)	5.4 (34)	5.7 (340)
	5.8 (42)	5.9 (95)	5.6 (35)	
Lateral flower of same	5.1 (48)	5.2 (48)	4.9 (29)	5.2 (204)
	5.3 (33)	5.3 (27)	5.5 (19)	
Accessory of this lateral	6.1 (3)	5.0 (2)	—	5.75 (11)
	5 (1)	6 (1)	6.0 (4)	
Second accessory of main flower	5.3 (4)	5.5 (6)	5.7 (7)	5.5 (22)
	5 (1)	5.3 (3)	6 (1)	
Lateral flower of same	—	—	—	5.1 (5)
	—	—	5.1 (5)	

In the table above the average floral number (of calyx, corolla, and two stamen whorls) is given; the figures in brackets indicate the numbers of observed flowers. The first line is from the observations in 1928, the second from those in 1929.

We see that there is a well defined, gradual variation, which is the same in the two years and in the three forms; the forms are very similar in this respect and only differ by the fact that the shortstyled plants are somewhat weaker.

The graduation may be described as follows: the three median flowers show, in the order in which they are developed, a diminishing strength; the lateral flowers are weaker that their median flower, and the accessory flowers of the laterals are remarkable by the fact they are again much stronger, nearly equal to the main flower.

The idea of a "normal" number for *Lythrum*, a number that is a part of an inherited diagram, does not seem appropriate in view of these facts. The individual flowers vary in their numbers from 4 to 8. The number for any given flower is determined by its individual strength, which partly depends on the position in the partial inflorescence.

It is the same as the well known fact that so often the first flowers in inflorescences are pleiomerous, the last ones meiomerous; only here this is repeated many times, in one single inflorescence, viz as often as there are partial inflorescences.

The main object of this paragraph is however the study of the heteromerous flowers in connection with meristic variation. To give a survey of the phenomena to be seen in *Lythrum* I give a series of camera lucida drawings from the preserved preparations, enlarged 7 times.

The drawings are arranged in such an order, that starting from a normal calyx sector, a multiplying of the sector is attained. As every abnormality, including those in a corolla sector, can be classed in this way, our series will give a fairly complete survey.

All drawings are made as seen from within the flower. As the floral parts become sufficiently transparent in glycerine, the underlying outer parts are also represented, in dotted lines; the veins in the filaments have been omitted, but those in the calyx have been figured. The petals, which had been removed, and which have as is usual in the family, very narrow insertions which leave no visible scars in the preparations, are omitted.

Fig. 1 is a calyx sector of a shortstyled flower; it has therefore been marked S. Two acute epicalyx leaves, and the corolla veins passing downward from these, are to be seen at the sides, the insertion of the petals was on these veins on the inner side of the calyx tube opposite the insertion of the epicalyx lobes at the outer side.

Between the two corolla veins we see the obtuse calyx lobe and the calyx vein; a few veinlets connect the calyx vein with the corolla veins. These veinlets were not always sufficiently clear in the preparations, so that sometimes they may have been overlooked.

The abnormality of this preparation consists in the presence of two long stamens instead of one. Ordinarily the single long stamen is inserted on the calyx vein. Here we see the two *m*-stamens on the corolla veins as usual, they are represented in their full length, their anthers having been lost.

Only the basal parts of the two *l*-stamens are visible and they are both inserted on the parenchyma next to the calyx vein, their filament veins being continued as separate veins in the calyx tube only to fuse lower down in the neighbourhood of the disc.

Fig. 2 is an analogous case, a single calyx leaf with two *l*-stamens. Here one of the two is inserted on the calyx vein, the other on a vein of its own.

Fig. 3 has the same conditions, only it is an L-flower, and the vein of the supernumerary episepalous stamen, which is an *m*-stamen here, soon fuses with the calyx vein.

Fig. 4 is almost the same case, but the supernumerary stamen vein does not fuse with the calyx vein, but with the adjoining corolla vein.

Fig. 5 is a case like that of fig. 2, but the two *l*-stamens are connate, with two anthers; their filament veins have been drawn as an exception. Notwithstanding their fusion, their decurrent veins are quite separate.

Here we see already that the vascular supply of the abnormal parts may exhibit considerable differences. The idea of Murbeck was, that fission and fusion of the original main vascular bundles were responsible for the appearance of new groups of organs or for the disappearance of existing ones. Our observations show that this idea is not borne out by the facts.

In these five cases it was the androecium that was pleiomerous; it may also be the calyx itself.

Fig. 6 has a set of normal stamens, *m l m*, but the calyx, though it shows one lobe with a single apex, has two veins. One strong one, the other somewhat weaker and not to be followed up to the apex. It is the strong one that bears the *l*-stamen.

Fig. 7 is similar: the supernumerary vein is here derived from a veinlet, coming from the epicalyx. Here the *l*-stamen is inserted between the two veins and runs towards the accessory one.

Fig. 8 has two equal calyx veins, and only one *l*. The corolla vein to the left (in the drawing) is also free.

Fig. 9 shows the combination of the two processes: if we consider the two calyx veins as a beginning of the doubling of the calyx, this is a sectorial variation. One of the calyx veins is derived from an epicalyx veinlet, but both veins bear a *m*-stamen.

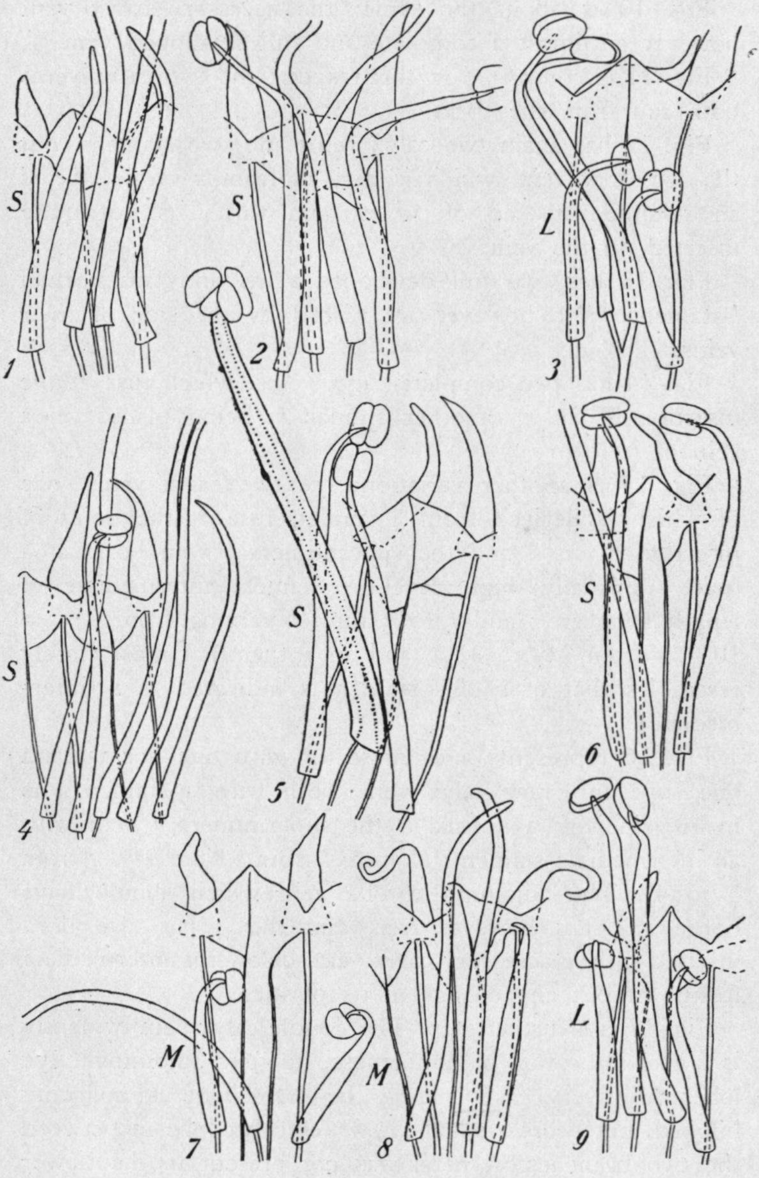

S
1
S
2
L
3
S
4
S
5
S
6
M
7
M
8
L
9

Fig. 10 is about the same; the accessory calyx vein however is almost a complete and full developed vein.

Fig. 11 is completed in this respect; the two calyx veins both run from the apex.

Fig. 12 has again two calyx veins and two stamens, but the accessory vein, which is derived from a veinlet, bears an *s*-stamen instead of an *m*, and this *s* is not quite inserted on the vein.

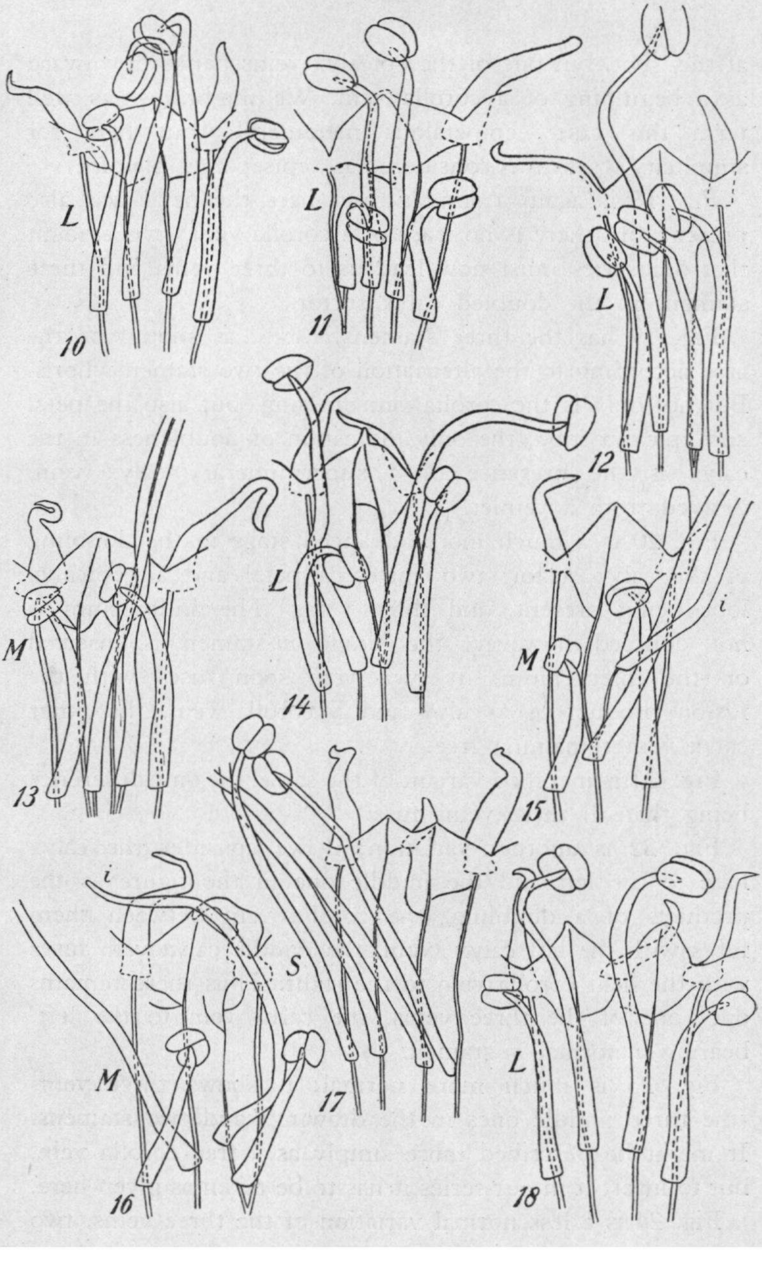
Fig. 13 has two full developed veins and two normal *l*-stamens, both however are placed by the side of their veins.

Fig. 14 has two complete calyx veins, which fuse at the insertion of an *m*, another similar *m* being placed on a vein of its own.

Fig. 15 is another variation; the two calyx veins, one of which is derived from a veinlet, fuse at the point of insertion of an *l*, and the supernumerary vein bears at a quite unusually high level a stamen, intermediate in length between *s* and *l* (6½ mm, *l* varying from 9½ to 10½, *s* from 2½ to 3½), and an anther that most closely resembles that of *l*; this stamen is indicated as *i* (intermediate).

Fig. 16 represents a calyx sector with one normal and one supernumerary calyx vein, both with a stamen; the main vein with a normal *l*, the supernumerary vein with an intermediate stamen *i* (7 mm; *l* from 9¼ to 9½, *s* from 3 to 4). The adjoining corolla vein which should have borne an *s*, is however free, and this *s* has also been inserted on the accessory calyx vein, below the intermediate form, without any change in its plastics.

Fig. 17 is a further step. The double calyx vein evidently is a real indication of doubleness, but two adjoining calyx lobes fuse very easily. Here the calyx lobe is not only bilobed, but bears a small „new" epicalyx lobe in between the two branches. A petal was not present in the flower


L
10
L
11
L
12
M
13
L
14
M
i
15
i
M
16
S
17
L
18

at this spot, but one of the epicalyx veins bends downward as a beginning of a corolla vein. We might just as well term this case „epipetalous meiomery", but here for simplicity's sake it is considered as „episepalous pleiomery".

Fig. 18 is again a similar case; here the petal was also present, but there is no trace of a corolla vein. It is evident that our series must now lead us to three veins and three stamens in the doubled calyx sector.

Fig. 19 has the three stamens, *l, s, l* as should be the case according to the alternation of the two stamen whorls. But not only is the corolla vein missing, but also the petal and epicalyx lobe; the only indication of doubleness in the calyx is the presence of a supernumerary calyx vein, derived from a veinlet.

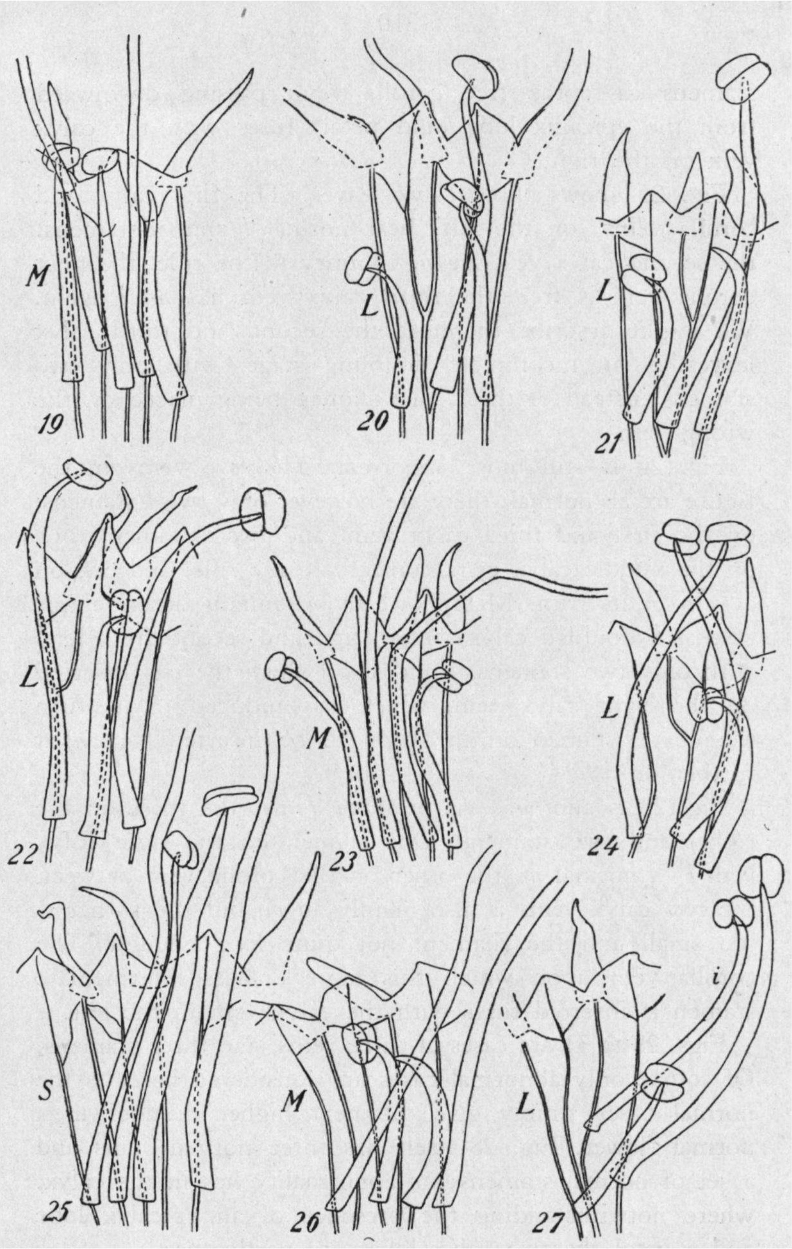
Fig. 20 is a much more advanced stage in the doubling of the calyx sector, two apices, a petal and an epicalyx lobe being present, and three veins. The androecium is not doubled however; the single *m*-stamen is inserted on the intervenium, its own vein soon fuses with the fusion product of a calyx and a corolla vein, the other calyx vein remaining free.

Fig. 21 is merely a variant of the same, the only difference being that all three veins fuse.

Fig. 22 is another variation; if we consider the calyx lobe to the left and the middle one in the figure as the products of a doubling, the corolla vein between them fuses with the left calyx vein, the middle calyx vein fuses with the next corolla vein to the right. Thus there remains only one of the three veins, the calyx vein to the left, bearing a normal *m*-stamen.

Fig. 23 is much more normal; it shows three veins (the three middle ones in the drawing) and two stamens. It might be described more simply as a free corolla vein, but to insert it in our series it has to be taken as given here.

Fig. 24 is a less normal variation of the three veins, two


M
19
L
20
L
21
L
22
M
23
L
24
S
25
M
26
i
L
27

stamens case; the free corolla vein, passing downward from the epicalyx lobe (and petal) fuses with the calyx vein on the right.

Fig. 25 shows three calyx leaves. The first calyx and corolla veins (on the left) bear normal *l* and *m*-stamens, the second calyx vein an *m*, contrary to the rule, the next corolla vein is free, the third calyx vein has an *l* again. We might describe therefore the second and third calyx leaves as an incomplete doubling stage, with only two stamens instead of three, one stamen being placed on the wrong vein.

Fig. 26 is still more abnormal. The five veins in the figure are all normal; there are however only two *l*-stamens, on the first and third calyx vein, and two *s*-stamens, one on the middle calyx vein, contrary to the rule, and one on a vein of its own. Metaphorically we might describe this case as a doubled calyx sector (first and second from left) with only two stamens, *l* and *s*, of which the *s* is inserted on the right calyx vein, which has induced in its turn the next *s*-stamen on the right to be inserted somewhat further on.

Fig. 27 is another case of three veins (the three on the right) and two stamens. One stamen on the right calyx vein is a normal *m*, the other on the corolla vein between the two calyx veins is also mainly an *m*, but the anther is too small and the filament not quite long enough. The corolla vein upon which this more or less intermediate stamen is inserted fuses with the calyx vein to the left.

Figs. 28 to 31 are cases of three veins, and three stamens. Of course only abnormal cases are considered here, as the normal cases simply give the next higher number in a normal flower. Fig. 28 itself has three normal veins and a set of normal stamens; its abnormality lies in the calyx, where notwithstanding the presence of an epicalyx lobe and a petal the two calyx lobes are partly fused.

Fig. 29 is normal in calyx and corolla, but the middle stamen which should have been an *s*, is differentiated as a normal *m*.

Fig. 30 combines the abnormalities of the two preceding cases; the calyx lobes are entirely connate, with a single apex; epicalyx lobe and petal are still present. The left calyx vein, which should have borne an *m*, bears however an *s*.

Fig. 31 is less normal; of the two calyx veins the left one soon fuses with a corolla vein to the left. In most flowers with such a fusing vein the correlated episepalous stamen is simply absent; here we have on the contrary lower down in the calyx tube a supernumerary *s*-stamen, so that three of them are placed next to each other.

Fig. 32 is a single case of three veins, and four stamens. The calyx lobe is apparently simple, its two calyx veins bear two normal *l*-stamens, between which on a vein of their own two stamens are inserted, one *m* at the normal level, one additional *l* much higher. As there is no additional epicalyx lobe nor a petal, one might be inclined to suppose that the phyllome which ought to have given rise to a petal had been differentiated into an *l*-stamen.

Figs. 33 to 35 finally are cases which only fit into our series as triplications of a calyx sector. In fig. 33 the veins are about normal, but the five veins of the three middle calyx leaves and the petals between them only bear three stamens, in a normal *m*, *s*, *m* sequence. The two corolla veins are free and fuse with a calyx vein to the left, the middle *s*-stamen is borne by a calyx vein, contrary to the rule. This stamen is however somewhat too well developed.

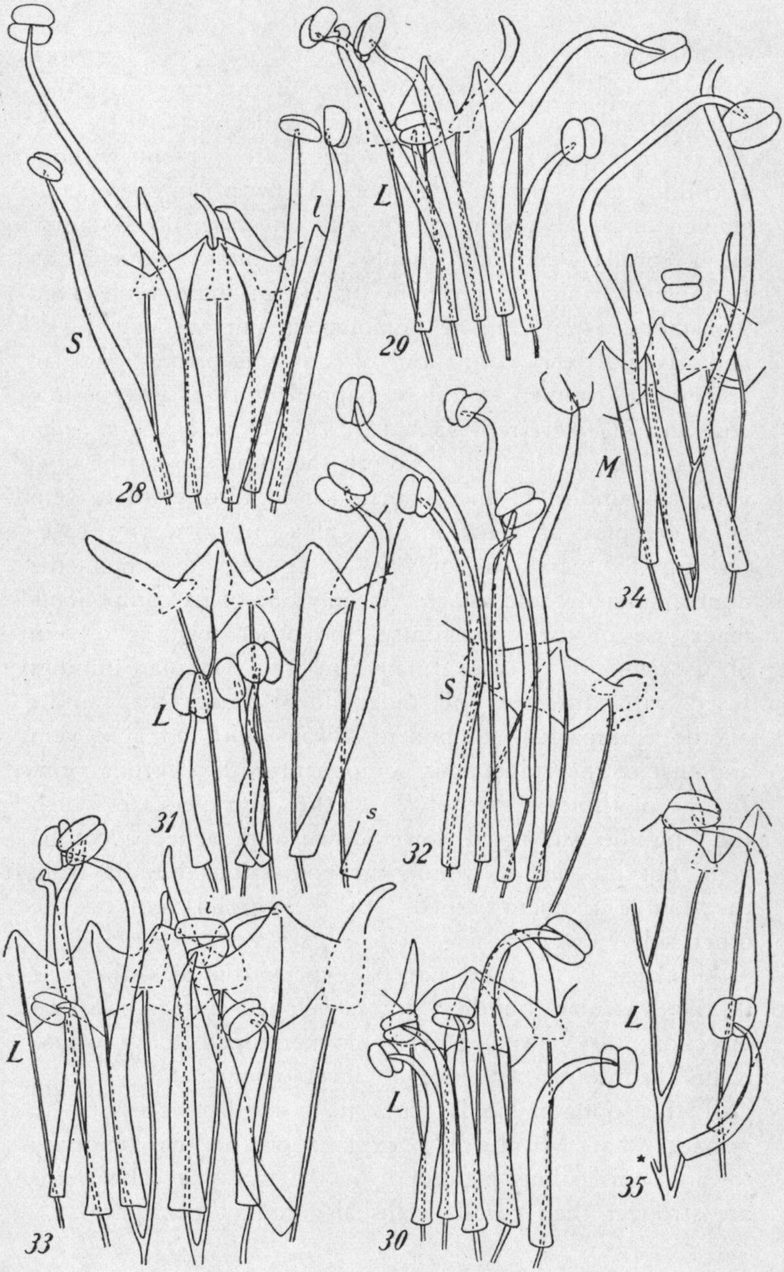
Fig. 34 has likewise five veins and three stamens, *l*, *s*, 1 in due alternation. This has been reached here in a different way from that in the preceding case, as all three middle veins fuse and together bear one normal *s*. (The anther of this *s* laid loose in the preparation and has been drawn so).

Fig. 35 shows a fusion of three veins, viz., two corolla veins, of which the left one is only partly represented, its epicalyx lobe being torn off, and a calyx vein. The common base of the three veins also receives the short veinlets of two normal *s*-stamens, one at the point marked with an asterisk and one being represented in the figure. To describe this case in terms of episepalous pleiomery we are obliged to consider the two calyx leaves of the figure and a third one still more to the left as a triplication of a calyx sector with four stamens instead of five, the *m*-stamen opposite the middle calyx vein being wanting.

The main impression of a perusal of this series of 35 cases will perhaps be, that the chosen arrangement is not a natural one. Yet quite the same impression would be obtained by any other arrangement, e. g. in terms of a vanishing corolla sector.

This is in no respect astonishing: the arrangement in a certain order would only be natural and logical when it was the representation of the stages of a natural process in the plant, a progressive fission or fusion. When such a progressive process does not exist, it is quite natural that the intermediate stages, being the result of accidental heteromerous combinations, may be in all respects irregular. It is the same conclusion as that at which Murbeck arrived in *Comarum* and *Alchemilla,* that „new" organs could arise in a number of ways, as fission parts of quite different organs.

As our drawings give much information about the distribution of the veins in the calyx tube, I might here say a few words about Murbeck's idea that the supposed processes could be brought about by the fission and fusion of the main vascular bundles. I trust that I may say that my material proves that this idea is not to be upheld. Throughout the whole series we see that the regularity of the arrangement of the organs is greater that


S
l
28
L
29
M
34
L
31
s
S
32
i
L
33
L
30
L
*
35

of the veins; the case of one calyx vein and two episepalous stamens (fig. 1—5) was convincing in this respect. Other cases which may be cited in this connection are fig. 18, where an epicalyx lobe and a petal are present without a corolla vein; figs. 25, 26, 30, 33 with an epipetalous stamen on a calyx vein, or 29 with an episepalous stamen on a corolla vein, and finally the connate stamens, an example of which is given in fig. 5. Of these I observed 9 instances, 4 of connate homologous stamens, like fig. 5 and five of the connation of an episepalous and an epipetalous stamen; it thus happened that all possible combinations were represented ($l + l$, $l + m$, $l + s$, $m + m$, $m + k$, $s + s$). In only two of the nine cases the two vascular bundles of the filament fused into a single vein or a complex of veins in the calyx tube; in two cases (cf. fig. 5) there was only a single vein to which the double stamen could attach, yet only one of its components made use of the opportunity, the other forming a vein of its own. In 5 cases finally the two vascular bundles fused with different and independent veins, the bundle of the episepalous component always with a calyx vein and that of the epipetalous component with a corolla vein. In one of these, a case of $l + s$, the calyx vein, to which the l-bundle was fused, lower down approached a corolla vein, not the one to which the epipetalous bundle from the double filament joined, but the corolla vein on the other side.

All these facts could not be expected to be otherwise if the vascular bundles are developed in a basipetal direction; the view of Murbeck mentioned above would claim the reverse sequence of development.

If this opinion holds true, it is hardly necessary to remark, that Murbeck's explanation of the tendency towards episepalous pleiomery by the fact that calyx veins are stronger than corolla veins also cannot be right.

Now in *Lythrum* this explanation entirely loses its foundation. In our figures we see that the corolla veins are of about constant size throughout the calyx tube from the epicalyx lobe to the disc. The calyx veins are much thinner in the calyx lobe, but on passing downward gradually increase in strength. At the level of insertion of the androecium the two sets are of about equal size; if we examine the preparations under a higher power we see that at this level the corolla veins are either equal to or somewhat thicker than the calyx veins. Yet episepalous pleiomery prevails in *Lythrum* as strikingly as in Murbeck's examples, so there must be another cause for the phenomenon.

Our material may perhaps further cast some light on the problems of whorl formation in the flower. According to the view set forth on p. 185, the successive whorls are to a certain extent formed independently, each whorl arising by the linking up of a number of phyllomes, which are already present. The number of members in a whorl certainly is influenced, but not wholly determined by that of the next lower whorl.

In this material we have in the first place the question of sectorial or non-sectorial arrangement of abnormalities. I contended above that there is only a certain tendency towards sectorial arrangement, but that in the literature this tendency generally is much overrated, owing to the fact that the pleiomerous and meiomerous flowers are considered to have a complete set of abnormalities throughout all the whorls, in a sectorial arrangement.

In really abnormal, heteromerous flowers I observed:
one abnormality ¹) in the flower .... 71 times

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¹) Only partial meristic variations, or the beginning of this variation are here counted as abnormalities. A calyx leaf with two veins, whether equal or unequal, has been considered as an abnormality. Cases in which there were supernumerary petals (14) are

two abnormalities on the same radius	38 times
two abnormalities on different radii	16 times
three abnormalities on different radii	4 times.

We see that the non-sectorial variations are in the majority; 115 against 76 sectorial cases. This I believe will be confirmed in other plants. From the conception of whorl formation as given above, this is what might have been expected; a certain tendency towards sectorial arrangement being the result of the influence of lower on higher whorls, without being so strong as to prevent the occurrence of abnormalities on different radii.

The heteromerous flower may however teach us more about whorl formation, by the way in which the whorls are adjusted to each other. I shall confine my arguments to the adjustment of the androecium to the perianth, because of the difficulty of judging the calyx and corolla numbers in some cases.

One supernumerary stamen in the flower was observed 51 times. In 48 of these cases the accessory stamen was an epipetalous one, i. e. a member of the longest set, all cases like the figs. 1—5, 9, 10, 11, 13, 14, 17. In only three cases was there a supernumerary shorter stamen; on a supernumerary calyx vein (fig. 12) or merely near a corolla vein.

The relation of these frequencies confirms Murbeck's conclusion, that episepalous pleiomery is more frequent than epipetalous pleiomery; in the androecium 6,5 and 5,4 are more probable than 5,6 and 4,5.

One missing stamen was observed in 32 cases; in 28 of these flowers it was an epipetalous stamen that was absent (cf. fig. 8, 18, 23). Here we have the same; 6,5 is more probable than 5,6.

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counted; missing petals were not considered, as there was always the uncertainty that the petal might have been destroyed and the scar, which is hardly discernible even in the fresh material overlooked.

Two supernumerary stamens were observed in 8 flowers. Five of them still had an androecium of two isomerous whorls. In four of the five this was arrived at by the insertion of three stamens on a (partly doubled) calyx sector, two longer and one shorter in between. In such a way the alternation of the two stamen whorls was also maintained. The fifth flower had two *l*-stamens on a calyx vein, and two *s* on an adjoining corolla vein; here the alternation was therefore disturbed.

The three remaining flowers had two additional longer stamens, owing to the development of two different calyx sectors, each with two longer stamens. This therefore represents a twofold episepalous pleiomery.

The case of two missing stamens was observed 13 times. Nine of these flowers had two isomerous stamen whorls, and in eight of these the alternation of the two whorls was perfectly regular; this was obtained either by the fact that two free veins were adjoining (cf. fig. 22) or in a similar way (fig. 20, 34). In the ninth flower there was no regular alternation, as an episepalous stamen was missing in one sector (fig. 35), an epipetalous one in quite another.

Of the remaining four flowers two had a twofold epipetalous meiomery owing to the presence of two different free corolla veins, and one practically exhibited a regular alternation again but for the circumstance that one stamen, which ought to have been an epipetalous one according to the alternation of stamens, but was inserted on a calyx vein (fig. 33), was of intermediate plastics.

We see therefore that in cases where the number of stamens does not agree with the number of perianth leaves, the alternation of the stamen whorls is yet kept up as much as possible. At the same time we see that the longer and shorter stamens are as much as possible inserted on the related veins, the longer on calyx, the shorter on corolla veins.

Three supernumerary stamens occurred twice: once by the development of four stamens opposite one (doubled) calyx sector (fig. 32) and once by the presence of two doubled calyx sectors, one with *l*, *m*, *l* and one with *l*, *l* as stamens.

Three stamens short also occurred twice: in both cases the alternation of the stamen whorls was maintained as far as possible, though of course with an odd number of stamens one whorl must have two stamens next to each other. In one flower there were four adjoining veins, together possessing one single stamen, in the other there were two abnormal sectors, drawn in fig. 21 and 27. In 21 the preserved alternation is evident; in 27 we have the position where the two equal stamens should be next to each other, instead of which one stamen is intermediate in its plastics.

These cases we see only confirm the conclusions drawn above.

We now have still to make some remarks about the insertion of the stamens on the veins. That longer stamens are attached to calyx, shorter ones to corolla veins is doubtless the rule; it is however not without exceptions.

In the first place we have stamens for which no vein is provided, as in figs. 2, 3, 5, 19 or 32. These stamens are simply inserted on the intervenium, and form a decurrent vein of their own.

In other cases there is only a vein of the „wrong" kind provided for them, and then they may unite to this, as in fig. 29 and 30.

Finally they may for some unknown reason become inserted in an unusual way, like the short stamen on the right in 16, or the *l*-stamen in 7, or the two in 13. Two equal stamens seem to be separated by a certain distance, cf. fig. 1 and 26.

A shorter stamen on a calyx vein, or a longer one on a corolla vein also sometimes occurred in otherwise isomerous flowers, which therefore came to have formulae for perianth and androecium such as 6,6, 5,7 or 6,6, 7,5. In these cases the insertion of the stamens might be perfectly normal but for the exception of the one stamen on the wrong vein. In other cases the whole arrangement was more or less disturbed.

The fact that a stamen on a calyx vein may be differentiated as an epipetalous stamen and reversely, which is fully established by the cases I have seen, deserves special attention; it proves that it is not the insertion on a certain vein that determines the differentiation. It points clearly to the correctness of the supposition made above, that the formation of the stamen whorls is to a certain extent independent of the perianth, but that the outer and longer stamens have a great affinity for the calyx veins and attach their vascular bundles by preference to them, whereas the inner and shorter stamens have similar affinity for the corolla veins.

This conclusion is corroborated by the following observation. If the vein, to which a stamen is attached, was able to affect the differentiation of the stamen, we must expect that it would be the stamens on a „wrong" vein, that would furnish the cases of intermediate stages between episepalous and epipetalous plastics.

This however is not the case; in such flowers as were figured in 16, 29 and 30, the stamen on the wrong vein is perfectly normal. Real transitional stages between episepalous and epipetalous stamens were present in 15 cases in my material. In 9 of them it was in heteromerous flowers with an odd number of stamens, so that the two stamen whorls had to differ in number. The intermediate form always stood between an episepalous and an epipetalous stamen (cf. fig. 15, 16, 27); the insertion was very different.

In two other flowers the stamen whorls were equal in number but they were both oligomerous as compared with the perianth; the intermediate stamen in both stood on that side of the flower where three veins had together only one stamen (cf. fig. 33). In only four isomerous flowers of the great number I inspected I found intermediate stages, one in each; these were all normally inserted on the correct vein.

These facts give a strong impression that it is the whorl formation which decides the plastics of the stamens, and that where this formation is irregular, there is much more chance that a young stamen will be affected by both the tendencies and will result in being an intermediate form.

The last topic I have to deal with from my observations on *Lythrum* are the twin flowers, in connection with the coalescence theory of De Candolle.

In the few (six) instances of twin flowers I met with, the difference between these and the normal simple flowers was so clear, that a doubt as to the category could never rise. Yet there was a slight overlapping in the floral number, as the normal flowers went up to 8, and the floral number of the twins varied from 8 to 16.

The twins however, which were all due to the lateral fusion of flowers, were extended in a lateral direction, so that their calyx tube had an elliptical transverse section; in some there was on the front and back sides a median, inwardly turned fold in the calyx tube. Only two possessed a single gynoecium, the others had two or three in a transverse row. The subtending bracts in two flowers were simple, three flowers had two subtending bracts, one had three.

In view of the marked distinction between these twins and the normal flowers the idea, that the pleiomerous normal flowers might owe their pleiomery to an analogous coalescence is not to be held.

§ 9. Summary.

1. The different explanations, found in botanical literature for meristic variation in flowers are reviewed and discussed. The result of these considerations is that only the original variation of Eichler is able to give a satisfactory explanation of the facts, i. e. the supposition that meristic variation in regular flowers is due to phyllotactical differences, whereas in zygomorphic flowers the same holds true, with the apparent exception that a pseudomeiomery may be caused by abortion or by fusion.

2. The rejected views are:

the explanation of pleiomery by fission, dedoublement (either taken as a phylogenetic or as an ontogenetic process) and reversely meiomery by fusion;

the explanation of meiomery by abortion of organs;

the explanation of pleiomery by the intercalation of sectors in the floral receptacle, and reversely of meiomery by omission of such sectors;

the explanation of pleiomery by coalescence of flowers, synanthy or gamogemmie.

3. On the basis of original variation the following facts, connected with meristic variation, may be explained:

that generally high numbers vary more than low numbers;

that nutrition has a marked influence on meristic variation;

that in many species intermediate stages between one and two organs occur in the form of broadened or bilobed members;

that these transition stages may be classed in a continuous series, from which however it is not to be ascertained whether the series represents the doubling of one, or the fusion of two phyllomes;

that the middle stages of such a series are more varying in character than the first or last;

that supernumerary organs are more frequent in a calyx sector (episepalous pleiomery or epipetalous meiomery) than in a corolla sector (episepalous meiomery or epipetalous pleiomery);

that terminal flowers in some plants have a different floral number from that of the lateral flowers of the same plant, a difference which is especially striking in terminal peloria, which are formed on a stem much exceeding the lateral branches in strength (Digitalis).

4. The Polygonaceous flower, which has played an important role in the literature on meristic variation is utterly unsuitable for this kind of investigation, so long as we cannot distinguish between the several processes affecting the floral number.

5. The flower of Lythrum confirms several of the facts enumerated above under 3.

The observed twin flowers showed no transition to the pleiomerous flowers; this is to be expected when we discard the coalescence theory for pleiomery.

The observed abnormal flowers made it clear that the irregularity of the vascular supply of the intermediate stages is greater than that of these stages themselves: this gives a new confirmation of the view that leaf traces are formed basipetally.

The same abnormal flowers suggest the following conceptions of whorl formation in the flower.

Every floral whorl is formed anew by the linking up of a certain number of preexistent phyllomes. The common isomery of flowers may be the outcome of the influence of lower whorls on the formation of higher ones.

The morphogenetic forces are different in the different zones; whether a stamen is differentiated as episepalous or as epipetalous does not depend on the insertion of the stamen on a calyx or a corolla vein, but on the morphogenetic forces of the whorl to which it belongs.

Once being determined, which happens very early, before the vascular tissue is induced, the episepalous stamen has a strong affinity for calyx veins, the epipetalous for corolla veins.

If there are two more stamens than perianth leaves, the most common solution is that three of them are associated with a single calyx sector; if there are two stamens short, two adjoining veins usually remain free; in such a way in both cases the alternation of the stamen whorls is maintained as well as the insertion on the appropriate veins.

In such cases where the number of stamens is odd, there is more chance than elsewhere, that one single stamen will show intermediate plastics, as a consequence of the fact that the formation of two whorls in the androecium meets with a difficulty at one point.

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Groningen, January 1932.

Postscript. I received the interesting article of H. J. Lam, Beiträge zur Morphologie der dreizähligen Burseraceae-Canarieae, Ann. de Buitenzorg 42, 1931, p. 23 when my manuscript was ready for the press.

Lam examined a great number of flowers of one single individual of *Canarium decumanum* as to their meristic variation, and to my great satisfaction I saw that the outcome of his investigation is that the observed facts are not to be explained by the theories of Goebel and Murbeck, but that on the contrary the original variation of Eichler is to be adopted (p. 49).

So far the agreement of the present paper with that of Lam is very close. A difference is however to be found in the explanation of the sectorial arrangement of abnormalities, which Lam considers to be caused by the course of the vascular bundles.

As I have previously dealt with the same view, held by Murbeck, I need here only call attention to the arguments already brought forward against it; moreover in the *Canarium* flower we again see that the course of the stamen traces is decidedly less regular than the distribution of the stamens themselves (Pl. 7, fig. 45D, 46), a fact which again corroborates Nägeli's thesis of the basipetal development of leaf traces.

Groningen, February 1932.

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