ON THE PERIANTH AESTIVATION IN THE PORTULACACEAE AND THE BASELLACEAE.

by

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Introduction. In my paper on the corolla aestivation (5) I expounded that a serious difficulty for the spiral theory of the flower might be found in the perianth aestivation of the *Portulacaceae* and *Basellaceae* as described by Eichler (1, II, p. 125, 128). The quincuncial arrangement of this perianth namely does not form the continuation of the spiral phyllotaxis to be assumed in the four preceding decussate phyllomes of prophylls and involucre.

Our fig. 1 A, a floral diagram of *Calandrinia procumbens* by

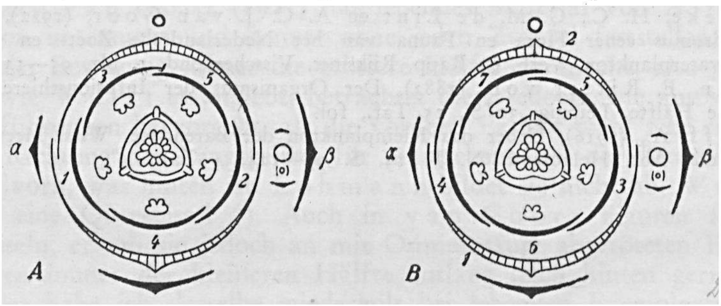

Fig. 1. *Calandrinia procumbens.* A floral diagram from Eichler (1, II, p. 125, fig. 47A); B the same with tepals numbered according to the spiral phyllotaxis of the preceding phyllomes.

Eichler, will make this clear. As the anterior involucral bract overlaps the posterior one on both sides, the four decussate phyllomes constitute a spiral (cf. Schoute, 4) which runs opisthodromously from α to β, then to the anterior bract and so to the posterior one; on continuing this spiral we successively reach the tepals 2, 1, 5, 4 and 3. Yet the correctness of these numbers seems to follow from the aestivation as stated by Eichler.

In order to investigate the causes of this curious disagreement I examined a number of plants. Before proceeding to the description of my observations I want to remark that my notation will be different from that of Eichler. The two involucral bracts will be denoted as 1 and 2, and the tepals as 3 — 7. These numbers will be given according to the supposed spiral, irrespective of the aestivation: Fig. 1 B will illustrate this.

From the diagrams it will be clear that the only difficulty is presented by the posterior edge between 5 and 7; here we find a metatopic 7/5 overlapping whereas all other edges have a eutopic aestivation. It is therefore to this critical edge that we shall have to pay attention in the first place.

When in the present paper the terms involucre and perianth are used for what Eichler called calyx and corolla, this is not an expression of an individual judgment on this difficult question, but only the outcome of the wish to be in accord with the modern authors (Franz, 2, Pax and Hoffmann, 3).

Six species having been examined this paper will be divided into seven paragraphs, the last one reserved for the discussion.

§ 1. **Calandrina speciosa.** Three cultures were examined, the seeds of which had been received in the Groningen Hortus under three different names. As there was no difference in the results, they are treated here as a whole.

The cotyledons are followed by long and slender leaves with a decussate phyllotaxis. It is however not difficult to determine the original spiral from the fact that the opposed leaves differ somewhat in size. Higher up the phyllotaxis gradually changes into a spiral one which is the continuation of the spiral as determined below.

The main axis is terminated by a flower. On the highest foliage leaf there follows with the same divergence the involucral bract 1. As 1 and 2 are broad and nearly flat, the involucre as a whole is strongly flattened in the bud condition. In this way the critical edge may perhaps come rather early into contact with 2.

A few of the highest foliage leaves subtend cincinni, that of the highest leaf being the strongest. The terminal flower is related to this highest cincinnus as if it were its first flower.

In the cincinni every flower is preceded by a small sterile lower bract and a large fertile higher one; the two bracts converge at the back side. There can be no doubt that the small one is an α- and the large one a β-prophyll.

The junction of the involucre with the prophylls, which Eichler describes as rectangular, was constantly found somewhat different in my material, as 1 was obliquely anterior, approached to *α*. This fact should remove the last doubt as to the correct determination of the prophylls.

The perianth aestivation was determined in 57 main flowers and in 100 cincinnus flowers. In all these the edges 3/5 and 4/7 were throughout eutopic; in 3—6 and 4—6 there were a few metatopies, 4 of 6/3 and 5 of 6/4. The critical edge behaved quite differently; in the main flowers it had 21 times 5/7 and 36 7/5 and in the cincinnus flowers it was 49 against 51.

In the cincinnus flowers the aestivation at this edge therefore is obviously determined by chance; in the main flowers there is a majority of the metatopic cases which is however not very strong and the meaning of which may be discussed later on.

§ 2. **Calandrinia grandiflora.** The fleshy cotyledons are followed by much larger fleshy foliage leaves which immediately show a spiral phyllotaxis; it may be remarked that the two cotyledons are also not of the same size, and that the smaller one takes the place of number 1, the larger that of number 2 in the spiral of the subsequent leaves.

The flowers are borne in exactly the same way and with the same junction as in *C. speciosa,* as terminal and as cincinnus flowers. A striking difference however is that the involucre is quite roundish in the bud so that there is no reason to expect a contact of a peculiar kind between the critical edge and bract 2.

There were observed 25 main flowers and 50 lateral ones; at the critical edge 7/5 was observed 3 times in the main and 9 times in the cincinnus flowers, against 22 and 41 eutopic cases; the other edges were always eutopic except for one 6/3 and one 6/4. A strong preponderance of eutopic aestivation, even at the critical edge is therefore beyond doubt.

§ 3. **Portulacca grandiflora.** The cotyledons are followed by a few pairs of decussate leaves; the pairs are however soon dissolved in the usual way into a transition to the normal spiral phyllotaxis of the higher leaves.

The shoot and its lateral branches all terminate in a flower under which a false whorl of 5—10, usually 8 foliage leaves is formed. Between the false whorl and the involucre of the flower there are mostly two small bracts each subtending a lateral flower. The same normal spiral is to be followed undisturbedly from the scattered leaves through the false whorl and the bracts up to the involucral bract 1. The two lateral flowers differ in size, that from the highest bract being this time the smallest.

All flower buds are quite roundish so that the development of the tepals will not have been influenced by the involucre form.

There were examined 100 terminal flowers in the expanding bud stage; in full anthesis the aestivation is either partly lost or in any case unreliable. The edges 3/5, 4/6, 3/6 and 4/7 were eutopic without a single exception; the critical edge 5—7 on the contrary was eutopic 5/7 in only 30 cases, metatopic 7/5 in 66 cases and for the remaining four cases the overlapping was eutopic in the basal part of the tepals, metatopic in the apical part.

Without any apparent reason we have therefore in this plant a marked preponderance of the metatopic condition described by Eichler as characteristic for the family.

§ 4. **Claytonia sibirica.** From the subterranean parts of this perennial plant a number of flowering shoots arise, each bearing two large free prophylls.

The inflorescences borne by these flowering shoots have been described by Wydler (6, p. 348 and 7, p. 329) and by Franz (2, p. 5). For our purpose however we need some facts which are not reported there, so that we shall now have to go into some detail.

From the axils of the two large prophylls which I shall call A and B two cincinni may arise: that in the axil of B is stronger and sometimes the only one present. The cincinnus from B was antidromous to the parent axis in all 29 observed cases; that from A was only homodromous in 2 and antidromous like that from B in 16 cases; we have here therefore one of the very rare cases where the axillary products of two prophylls are not each other's mirror image in their phyllotactical spiral [1]).

Both cincinni in the young stage are covered by the two prophylls α_1 and β_1 of their first flower; in the usual case A α_1 falls on the front side, B α_1, on the back side. From the axil of A α_1, a third cincinnus may develop which is antidromous to the A-cincinnus. All subsequent flowers only bear their β-prophylls, the α-prophylls being aborted.

The most important point for us is however the determination of the involucre junction with the prophylls.

According to Eichler all *Portulacaceae* show the same involucre junction, with bract 2 towards the axis (1, II. p. 125) and Franz follows him in this respect (2, p. 3); the conflicting statements in the literature on the reverse junction, with bract 1

[1]) Wydler writes (7, p. 330): "Bei den beiden oben genannten Arten" (i.e. *Cl. sibirica* and *Cl. perfoliata*) "glaube ich bei Doppelwickeln einige Mal Homodromie beider Zweige beobachtet zu haben".

towards the axis are claimed by both authors to be erroneous.

It is not the place here to institute an investigation into the mode of involucre junction in the whole family. But I might emphasize that in its generalization the quoted view is too excessive: both ways of junction actually are present in the family, and *Cl. sibirica* is an example of the impugned condition.

We may perhaps draw a parallel between the unusual distribution of the spiral directions in the cincinni members and the occurrence of two opposed involucre junctions: apparently the spiral direction is more variable in these plants than is usual in Dicotyledons.

The difference between the admitted mode of junction in *Calandrinia* and the impugned one in *Claytonia sibirica* is the more hidden from the eye as the apparent position of the young flower buds in the cincinnus is quite the same in both cases, the overlapping involucral bracts being placed to the outside of the double row of buds and somewhat towards the base of the inflorescence. The inner bract 2 is therefore more or less turned towards the next younger flower.

Our fig. 2 may illustrate this condition: A and C represent the

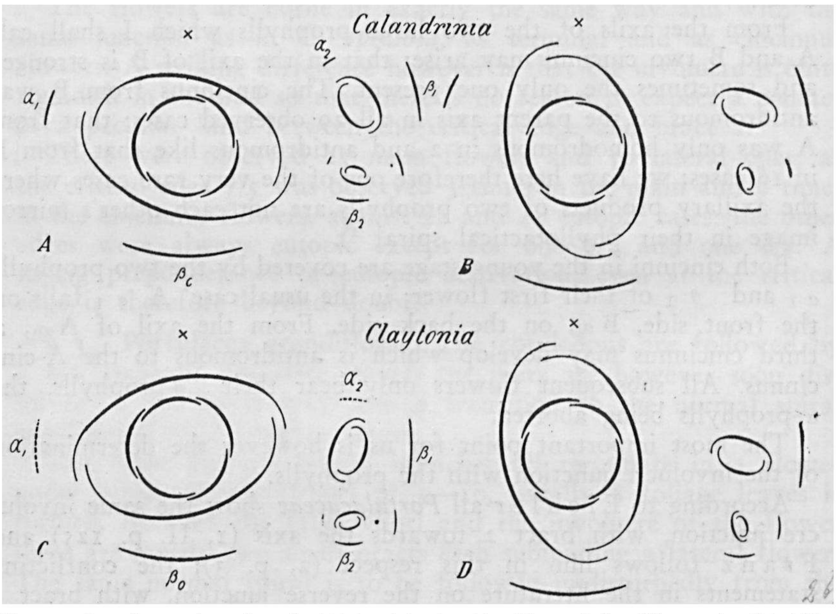

Fig. 2. Involucre junction in *Calandriania* (A, B) and in *Claytonia* (C, D). A and C actual diagrams of cincinni, B and D the same as they seem to be by the torsion of the pedicels.

actual diagram of the *Calandrinia* and the *Claytonia* cincinnus, B and D the same as seen when viewed on the top of the flower buds. It will be clear that the apparent condition of B and D can only be the result of a torsion of the pedicels, a torsion through 45° or 90°, but in a different direction in the two cases.

The real existence of these torsions in *Claytonia* can easily be observed from the longitudinal rows of stomata which are very conspicuous under the simplex. When controlled in this way it appeared that the midrib of involucral bract 1 is not truly adaxial but is somewhat approached to α, so that the whole phyllotaxis apart from the emprosthodromy is the exact analogue of that of *Calandrinia.*

It will be obvious from Fig. 2 that this mode of involucre junction entails a reverse spiral in the perianth, so that the aestivation at the critical edge would be determined as being metatopic when eutopic and conversely by anyone not aware of the different mode of junction.

The perianth aestivation was determined in 50 flowers. The edges 3-5, 4-6, 3-6 and 4-7 being nearly always eutopic, were not recorded in detail; the edge 5/7 only was always noted down. In the first 25 flowers it was 16 times 5/7 against 9 times 7/5; in the second lot it was 21 versus 4.

The preponderance of eutopy is therefore well marked.

§ 5. **Claytonia perfoliata.** The inflorescence of this much cultivated plant has much in common with that of the preceding species, but owing to a few additional difficulties it has given rise to much more comment.

The first of these is that the spurious axis of the cincinnus shows a curious distribution of longitudinal growth, most of its constituent parts remaining quite short whilst others elongate; in this way the spurious axis is set with groups of flowers in an irregular distribution. For our purpose this peculiar condition which has been fully recognized by W y d l e r (6, p. 348), is however not important.

The other difficulty is caused by the abortion of nearly all prophylls; not only α_2 and all subsequent α-prophylls are deficient, but also the β_1 and all following β's. The only secondary prophyll which usually remains is therefore α_1; when there are two cincinni there may be two of them, A α_1 and B α_1; in many cases even, one or both of these two may share the fate of their mates and disappear al together. In such inflorescences only A and B remain.

The A α_1 and B α_1 have been described by Wydler as of an uncertain nature. He writes: "Diese Vorblätter sind wegen ihrer eigenthümlichen Stellung etwas schwer unterzubringen; jedenfalls sind sie wohl als zweites Vorblatt der ersten Blüthe der Wickeln zu deuten" (7, p. 330). He is therefore inclined to consider them as β-prophylls. But in that case their position should be different: they are placed near the first cincinnus flower somewhat to the posterior side of the inflorescence and more or less opposite the second flower of the cincinnus.

This, and the consideration of the fact that in *Cl. sibirica* the α_1-prophyll is stronger than the β_1-prophyll and is situated in the same position as the single prophyll here, leave no room for doubt.

The cincinni may sometimes branch by the development of an α-flower, even in the more distal parts of the inflorescence; such an α-cincinnus may again be antidromous to its parent axis as in *Cl. sibirica*. Whether this condition is the rule here was not to be determined.

The involucre junction is the same as in *Cl. sibirica;* though the prophyll abortion impedes observation we may remark that the stoma rows lead the way from the midrib of bract 2 of a flower towards a point adjoining the insertion of the next older flower.

The perianth aestivation was determined in 50 flowers. The first 25 flowers yielded 12 cases of 5/7 and 13 of 7/5; in the second lot it was 13 versus 12. The other edges generally were eutopic but have not been recorded.

This aestivation at the critical edge gives a clear instance of a chance aestivation.

§ 6. **Basella rubra.** The inflorescences in this species are spikes with a terminal flower. The lateral flowers are entirely unsuited to our purpose, as neither the prophylls nor the involucral bracts reveal the spiral direction. The prophylls being inserted at the same level are both of the same small dimensions and have open aestivation; the two involucral bracts only meet each other at their apical parts, not at their edges.

The terminal flowers however are preceded by a variable number of bracts subtending the lateral flowers; these bracts always show a normal spiral phyllotaxis very clearly.

These terminal flowers differ from the lateral ones in their floral number. The involucre usually consists of two small outer bracts, with the shape and plastics of the bracteoles of the lateral flowers, and three larger bracts resembling the involucral bracts of the lateral flowers; the numbers however vary and transitional stages occur.

All these involucral bracts continue, without any alteration, the normal spiral of the lower floriparous bracts.

The perianth consists of 3-6 tepals, mostly of five; as however there are transitional stages between tepals and stamens, their number is not always to be determined. On the whole these tepals equally continue the same spiral phyllotaxis. Observation being rather difficult on account of the fleshy character of all phyllomes impeding the preparation, I was obliged to content myself with the determination of the perianth aestivation of ten pentamerous flowers.

Numbering the perianth as 6-10, after the five involucral bracts, the observed aestivation was:

edge	eutopic	metatopic	open
6—8	8½	½	1
7—9	10	0	0
8—10	5	2	3
6—9	10	0	0
7—10	10	0	0

We see that four of the five edges are strongly eutopic. It is again only the critical edge 8-10, which corresponds to 5-7 in the *Portulacaceae*, that we have some metatopies and open aestivations.

Though the available amount of evidence certainly is rather small, yet we get the strong impression that the spiral of the lower phyllomes is continued here too in the involucre as well as in the perianth, and that the contradictory statement for the perianth as given by Eichler is not well founded.

§ 7. **Discussion.** Since our observations described above pertain to five species of *Portulacaceae* and to only one of *Basellaceae* an extension especially of the latter number would have been very desirable. The only other species of the *Basellaceae* however which was at my disposition in a flowering state, *Ullucus tuberosus*, soon appeared to be quite unsuitable, as the lateral spikes do not possess a terminal flower and the lateral flowers can not be used, for the same reasons as in *Basella*.

The results obtained in the six species described above are remarkably divergent.

In one of them, *Claytonia perfoliata*, we met with a very neat case of a chance distributions of the aestivation at the critical edge, namely of 25 : 25.

In a second species, *Calandrinia speciosa,* it was nearly the same, 49 : 51 in the lateral and 21 : 36 in the terminal flowers; the advantage was here for the condition as stated by Eichler.

Of the remaining four species there is one more in favour of Eichler, namely *Portulacca grandiflora,* and three more or less against him. In *Portulacca grandiflora* out of 100 flowers we had 30 cases of 5/7 against 66 of 7/5 and 4 mixed cases. A difference of 16 from the mean in 100 observations is nearly five times the probable error, more than three times the mean error and is therefore rather well founded.

The remaining three species are however on the whole still much stronger against Eichler and in favour of a continued spiral phyllotaxis in the perianth. When we leave *Basella* out of consideration with its small number of observations, we have the two cases of *Claytonia sibirica* with 37 against 13 and of *Calandrinia grandiflora* with 63 against 12. For these species the statement of Eichler is beyond doubt contrary to nature.

Our first conclusion may therefore be that though the perianth aestivation as described by Eichler occurs without any doubt, it is not the prevailing rule, and that its reverse probably even occurs more frequently.

The clash between Eichler's statement and the spiral theory of the flower in this way loses its serious aspect; in so far our investigation has been successful.

It remains however highly remarkable that the aestivation at the critical edge differs so much from that at the other edges; instead of being eutopic throughout with a very few exceptional cases, it wavers between eutopy and metatopy in the different species.

An explanation of this curious fact is certainly out of my reach. In my paper on the corolla aestivation (5) we may however meet with a number of analogous phenomena. I described there for several species the fact that one edge of the corolla differed from the others in an analogous way. In most species this edge was 8-10 *(Passiflora coerulea, Candollea cuneiformis, Rosa canina,* several *Crassulaceae).*

In the discussion of the facts I related the predilection of this particular edge for metatopy with the fact that petals 8 and 10 are placed more or less over the often fertile bracteole β. When we now compare these two sets of cases, we cannot fail to remark a certain parallelism.

In *Portulacca* and its allies it is the third tepal 5 which lies with β in the same quinary parastichy and which becomes overlapped by the fifth tepal 7; in *Passiflora* and its companions it is the third petal 8 which lies with β in the same octonary parastichy and which becomes overlapped by the fifth petal 10.

Whether this parallel is due to any real congeniality of the underlying causes must be left out of consideration owing to lack of any means of further discrimination.

Summary.

1. The perianth aestivation of five species of *Portulacaceae* and of one of *Basellaceae* is described.

2. The aestivation at four of the five edges is throughout eutopic. The fifth edge, that between the third and the fifth tepal is very different in this respect and has been called therefore the critical edge.

3. In some species the aestivation at the critical edge shows a strong preponderance of eutopy; in others we meet with a chance distribution, in still others there is a certain preponderance of metatopy.

4. This fact is paralleled with the analogous fact that in some Dicotyledonous corollas the edge between the third and the fifth petal has a certain tendency to metatopy lacking at the other edges.

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