

ON THE CONTORT AESTIVATION OF THE ANDROECIUM OF SIDALCEA

by

J. C. SCHOUTE.

Since stamens nearly always have small insertions and terete filaments, the androecium rarely shows a lateral overlapping of its component parts: its "aestivation" is nearly always an apert one.

The genus *Sidalcea* amongst the *Malvaceae* is one of these exceptional cases, part of the androecium showing a well-developed contort aestivation.

The genus, established by A. Gray (3, p. 18), is characterized by a stamen column which not only at its summit bears a number of filaments, but which moreover on its outside bears five broad petaloid antepetalous lobes, each terminating in 4 to 8 filaments; these lobes are called the outer phalanges. The inner filaments are usually arranged in similar but smaller phalanges.

Now it is the outer phalanges which are contort in most or in all species of the genus¹⁾. About the contortion direction no indication has been given by Gray or any other author as far as I know; a diagram of *S. diploscypha* by Gray (4, pl. 120, fig. 1), copied by Eichler (2, p. 281, fig. 114), represents the contortion as parallel to that of the corolla. So I tried to determine the contortion direction myself, for which purpose a culture of *S. candida* was grown in the Groningen Hortus.

In my material the outer phalanges which are inserted in this species at the upper end of the stamen column, close under the inner phalanges, as a rule had six filaments each, united into three pairs. The pairs were of unequal length, the pair next to the overlapping edge being longest.

From the five overlapping edges a line was decurrent on the stamen column, in a transverse section these exactly antesepalous lines being visible as shallow grooves. Similar lines are drawn by Gray for *S. diploscypha*, not for *candida*.

¹⁾ In Pl. Fendl. (3) the contortion is only mentioned for the § 1, comprising the spp. *S. diploscypha*, *S. californica* and *S. delphinifolia*; in Gen. Fl. Am. Bor.-or. (4), p. 57, the contort aestivation is ascribed to the whole genus.

The contortion direction in agreement with Gray's diagram proved to be invariably the same as that of the subtending corolla; i.e. on a right contort corolla always followed right contort outer phalanges, and conversely. What we ought to know further for a description of this contortion is the calyx spiral direction. As however like in all *Malvaceae* the calyx has a valvate aestivation, its spiral direction, probably very clear during the developmental stages²⁾, can no longer directly be determined in the flowers or in the buds; moreover neither can it be determined indirectly, as prophylls and an involucre are wanting and the flowers in the simple racemes, as judged from the corolla contortion, are poecilodromous.

From the observations by Braun (1), Wydler (8, p. 126) and Eichler it has however been fully established that in the *Malvaceae* the corolla is heterotropic SW³⁾, and no doubt the same holds true for *Sidalcea*. We may therefore conclude that the outer stamen phalanges are heterotropic SW too.

The establishment of this fact is in so far important, as it furnishes us with a new opportunity of testing the validity of the explanation given earlier for the contortion direction in the heterotropic corolla (7, p. 41).

In the paper quoted this hypothesis was not only checked by a study of the deviations from contort aestivation in the individual flowers, but moreover it was put to the test by a comparison with the conditions to be found in other analogous contort organs, especially with the case of the heterotropic calyx aestivation of the *Cistaceae* (7, p. 43) and that of the heterotropic aestivation of the cyathium appendages of *Euphorbia*.

Here we have a third group of related phenomena and it is not difficult to prove that the outer phalanges, if the explanation for the heterotropic corolla aestivation be correct, only might be expected to be heterotropic SW contort, and not LW.

The salient point of the explanation was namely that the undetermined skewness tendency of any organ primordium was determined as to its direction by the presence of previously existing surrounding objects, occurring in an asymmetrical distribution. For the petals these objects were two sepals, for the inner sepals of the *Cistaceae*

²⁾ Payer (§) reports a quincuncial origin of the calyx for all *Malvaceae*; the number of genera Payer examined is eleven.

³⁾ Heterotropic (see Schoute, 7) = a contortion the direction of which changes with the phyllotactical spiral; heterotropic SW = when a right hand phyllotactical spiral gives a right contort whorl and reversely; heterotropic LW = when a right hand contortion is formed out of phyllomes with a left hand phyllotactical spiral and reversely.

they were the outer sepals and lower phyllomes; for the *Euphorbia* appendages they were the superposed involucre bracts.

For the outer stamen phalanges the only surrounding objects which reasonably can be taken into consideration are the petals. And as the phalanges are epipetalous, it is to be expected that every phalanx follows in skewness the petal under it.

The lopsidedness of the phalanges is in curious contrast to that of petals, as contort petals are always either equal-sided, or the overlapping half is smaller; in the phalanges on the contrary the overlapping side is enlarged.

The question might be raised whether the contortion of the petaloid phalanges might be used in dealing with the difficult problem of the number and position of the original units composing the androecium.

In *S. candida* the phalanges are clearly arranged in three whorls, one of the epipetalous outer phalanges with six filaments each, one of five episepalous phalanges with two filaments each and a third innermost whorl of five epipetalous phalanges with again two filaments each; the same arrangement therefore as drawn by Gray in his diagram of *S. diploscypha*.

This might quite well be taken as representing three original phyllome whorls; the corolla-like contort aestivation of the outer whorl would fit in very well with this view. We have to remember, however, that in some *Euphorbia* spp. the appendages of the commissural calyx glands, surely not originally phyllomes, have the same heterotropic aestivation.

In view of the many difficulties of the problem it may therefore be better to refrain from hasty conclusions.

In a quite recent paper Sanders (6) tries to solve the above problem about the Malvaceous androecium by observations on the course of the vascular bundles. She comes to the conclusion that in all *Malvaceae*, including *Sidalcea*, all filaments are due to the division of only five antepetalous stamens. This conclusion, being wholly based on the unwarranted belief that the morphological nature of a phyllome may be determined from the mode of insertion of its traces in the stem stele, in my opinion has to be discarded.

Groningen, July 1936.

Botanical Laboratory of the
Government University.

LITERATURE.

1. A. L. Braun, Ueber die gesetzlichen Drehungen im Pflanzenreiche, besonders diejenigen, welche an Blüten und Früchten vorkommen, *Flora*, 22, 1839, p. 311.
2. A. W. Eichler, *Blüthendiagramme II*, Leipzig 1878.
3. A. Gray, *Plantae Fendlerianae*, *Mem. Amer. Acad. of Arts and Sc.*, new ser. 4, 1849, p. 1.
4. —, *Genera Florae Americae Boreali-orientalis illustrata*, II, New York 1849.
5. J. B. Payer, *Traité d'organogénie de la fleur*, Paris 1857.
6. E. R. Saunders, On certain features of floral construction and arrangement in the Malvaceae, *Ann. of Bot.*, 50, 1936, p. 247.
7. J. C. Schoute, On corolla aestivation and phyllotaxis of floral phylomes, *Verh. Kon. Akad. v. Wetensch. Amsterdam*, 2nd sect. 34, 1935, No. 4.
8. H. Wydler, Die Knospelage der Blätter in übersichtlicher Zusammenstellung, *Flora* 34, 1851, p. 113.