Botany. — *On the Contort Corolla.* By J. C. SCHOUTE. (Preliminary communication, from a more extensive paper on the aestivation of the corolla).

(Communicated at the meeting of October 31, 1931.)

The contort aestivation of the corolla has until the present time received only scanty attention from botanists.

Since a short period of careful observation and accurate description by A. BRAUN [1]) and H. WYDLER [2]) hardly anything has followed and very few botanists have ever pondered about the contort aestivation as a curious and unexplained phenomenon, worthy of a special investigation.

In 1886 SCHUMANN published a paper on the mechanical causes of the corollar aestivation [3]); his idea about the contort aestivation is that it is caused by a rhythmic growth distribution in the floral receptacle. It is clear however that a rhythmic growth distribution in the receptacle or elsewhere, even if it had been actually observed, can never be the explanation of the contort condition. Growth processes in developing members are naturally always such as to bring about the adult condition; this needs no special investigation to be stated but is a logical postulate. A real explanation of the contort condition should make us understand why the distribution of growth is as it is.

The only other paper touching our problem, is as far as I know that of REINSCH of 1926 [4]). His conclusion about contort aestivation is that it is the outcome of the general symmetry of the flower, a conclusion that certainly does not bring us much nearer to a real understanding. REINSCH further follows the same line as SCHUMANN in so far as he derives the resulting aestivations from the distribution of active growth.

It is very remarkable that neither SCHUMANN nor REINSCH make any mention of the important fact, that there are two different kinds of contort

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[1]) A. BRAUN, Ueber die gesetzlichen Drehungen im Pflanzenreiche, besonders diejenigen, welche an Blüthen und Früchten vorkommen. Flora **22**, 1839, p. 311, report of meeting of Deutsche Naturforscher u. Aerzte in Freiburg i. B. 25 Sept. 1838. — A. BRAUN, Beitrag zur Feststellung natürlicher Gattungen unter den Sileneen. Flora **26**, 1843, p. 349.

[2]) H. WYDLER, Die Knospenlage der Blätter in übersichtlicher Zusammenstellung. Mitth. d. Berner naturforschenden Gesellschaft 1850 and Flora **34**, 1851, p. 113.

[3]) K. SCHUMANN, Die Aestivation der Blüthen und ihre mechanische Ursachen. Berichte d. D. Bot. Ges. **4**, 1886, p. 53.

[4]) J. REINSCH, Ueber die Entstehung der Aestivationsformen von Kelch und Blumenkrone dikotyler Pflanzen und über die Beziehungen der Deckungsweisen zur Gesamtsymmetrie der Blüte. Flora **121**, 1926, p. 77.

aestivation. Evidently their interest is wholly taken up by the developmental details, so that they have no eye left for more general facts.

Yet the nearly century old distinction of A. BRAUN between independent or constant convolution, which keeps the same direction in all flowers of a given species, and dependent or alternating convolution, which changes with the calyx spiral, is a natural and important one, and no explanation of convolution will ever be complete unless these remarkable facts are fully considered.

With the existence of two kinds of convolution these general facts are by no means exhausted. We may cite in the first place the constant relation between the calyx spiral and the direction of the dependent convolution. We always see namely that the petal before sepal 1 and 3 has its outward-turned margin before 1, its inward-turned one before 3. This relation was observed by BRAUN in his first mentioned paper, and confirmed in his later one and in that of WYDLER; but it seems never to have been made mention of in later years. In EICHLERs Blüthendiagramme we find indicated for all families with contort corolla dealt with, what the relation is; but not only do we miss the remark that it always turns out to be the same, but even in one case, that of *Statice* [1]) he states the reserve condition, the petal between sep. 1 and 3 having its outer margin before 3, without a single remark as to the peculiarity of the case.

A further noteworthy fact is that both kinds of contort corolla may occur in zygomorphic flowers. *Hemigraphis colorata* e.g. has a clearly bilabiate corolla with constantly left-hand [2]) contort aestivation; according to WYDLER and EICHLER [3]) the same holds good for many other *Acanthaceae*. Amongst the alternating contort corollas a striking case of zygomorphy is afforded by the *Trigoniaceae*. [4])

This fact is distinctly unfavourable to the idea of REINSCH that the aestivation depends on the general symmetry of the flower: in this respect it is remarkable that REINSCH denies the existance of zygomorphic contort corollas. [5])

A last group of facts worth mentioning is that the petals of contort corollas are often oblique, and in such cases the overlapping margins always seem to be the narrow halves, the inner halves being broader. This asymmetry, which has been described by WYDLER, SCHUMANN and CHURCH [6]), occurs just as well in constantly contort as in alternatingly

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[1]) EICHLER, Blüthendiagramme, Leipzig 1875-'78 I, p. 329.

[2]) Left-hand taken in the sense of EICHLER; the left margin of the petal, as seen from the outside of the flower, overlaps the neighbouring petal.

[3]) WYDLER l. c. p. 124; EICHLER I p. 218.

[4]) EICHLER II p. 343.

[5]) l. c. p. 113.

[6]) WYDLER, Kleinere Beiträge zur Kenntniss einheimischer Gewächse, Flora **42**, 1859, p. 359, SCHUMANN l. c. p. 65, A. H. CHURCH, Types of floral mechanism, I, Oxford 1908, p. 193.

contort corollas. What SCHUMANN writes, viz. that contort corollas always have oblique petals, is however, not true. In many cases the petals are quite symmetrical. REINSCH gives some instances [1]) and I myself observed some others, in both kinds of contort corollas. We may even in one genus have two species, one with oblique, the other with symmetrical petals. Instances of oblique petals are *Vinca maior* and *Tabernaemontana coronaria* with constant, *Linum austriacum, Oxalis floribunda, O. Ortgiesii* and *Plumbago Capensis* with alternating convolution; symmetrical petals are to be found in *Phlox paniculata* and *Armeria maritima* with constant, *Linum usitatissium, L. flavum, Gypsophila paniculata, Geranium sanguineum* and *Plumbago Larpentae* with alternating convolution.

My own researches on the contort corolla have so far chiefly dealt with alternating convolution, of which I had more material at hand.

About constant convolution I can add one observation only to our knowledge, viz. that in *Tabernaemontana coronaria* fl. pl. the supernumerary inner petals have just the same left-hand contort aestivation as the outer ones.

As constant convolution is not influenced by the varying calyx spiral, the cause of the convolution must lie in the corolla itself; it was this what BRAUN expressed in his term independent convolution. Evidently the petals themselves are inclined to a certain skewness, which may express itself in different sizes of the two halves, but which may just as easily only cause a different direction of the two margins, in otherwise symmetrical petals, one side being directed outward in the bud, the other side inward. We may compare this — though such a comparison gives no explanation whatever — with the righthandedness of man.

I will call this independent convolution in future autotropic, and the dependent form heterotropic convolution.

About heterotropic contort corollas I have made some more observations; before dealing with them however, I will give, as a starting point, the conclusions as to the origin of the heterotropic convolution I was brought to during my work.

Several of the best morphologists of the past firmly believed [2]) that all floral whorls are false, an opinion that has been abandoned in later years, chiefly because the developmental observations did not seem to support it. Now it has often been remarked that observations only show us rather late and advanced stages. If the old opinion still held good, we might

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[1]) l. c. p. 113.

[2]) VON MARTIUS, Ueber die Architektonik der Blumen, Isis 1829, p. 335; C. SCHIMPER, Beschreibung des *Symphytum Zeyheri*, Geigers Magazin für Pharmacie 1829, p. 83 and 84 of the offprint; A. BRAUN. Vergl. Unters. ü. d. Ordnung der Schuppen an den Tannenzapfen etc., Nova Acta A. C. L. C. N. C. **15**, I. 1831, p. 196; H. WYDLER l. c. 1851, p. 122, 124.

number the petals of a pentamerous corolla as 6—10, as has been done in fig. 1.

Comparison with fig. 2, a case which we have in some flowers e.g. several *Ternstroemiaceae,* shows that the difference between a eutopic corolla and a heterotropic contort corolla consists in a different overlapping at three edges, indicated in fig. 2 by asterisks. If the contort corolla is

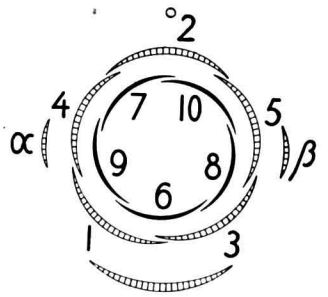

Fig. 1. Diagram of pentamerous flower with heterotropic contort corolla.

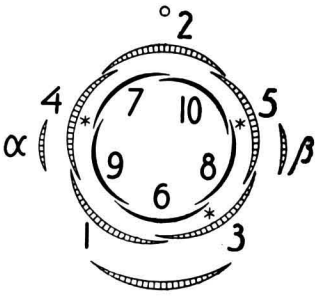

Fig. 2. Diagram of pentamerous flower with eutopic corolla.

originally spiral, at these three points the aestivation must arise the other way as it would have done in a eutopic case. We see at once that a more simple way of getting a similar result would have been a change at the two other edges; this would give what EICHLER mentions for *Statice,* the reverse relation between calyx spiral and convolution.

Now the supposition of a spiral origin of the apparently whorled corolla gives an easy clue as to the predominance of the common relation.

Amongst the petals 6 must be the eldest one. Supposing that it has a tendency to the same skewness as in the autotropic corolla, only not yet determined as to the right or left direction, we can easily see that it will find beneath it a skew base, a skew boundary to which it may join itself in its expansion process. The influence of this preexisting boundary may cause the young petal to choose between right and left. In the same way 7 may get a similar impulse from 2 and 4, and 8 from 3 and 5. This threefold stimulus may do for 9 and 10 too, which are taken along by 6, 7 and 8. If not, the corolla does not become contort at all.

This view granted for a while, the case of *Statice* becomes the more interesting. The evidence EICHLER brings consists in the words "wechselwendig nach dem langen Wege der Kelchspirale", which means in his terminology the reverse convolution of our fig. 1; and a diagram 168 A, both on p. 329 vol. I. The diagram is in accordance with the words; literature is not cited.

Long before EICHLER, in 1856 WYDLER [1]) described *Statice* in the same

[1]) H. WYDLER, Morphologische Notizen, Flora **39**, 1856, p. 39.

respect: with nearly the same term "nach dem langen Weg der vorausgehenden Blattspirale". In WYDLER's words this however means the reverse of what it does in EICHLER's. Perhaps EICHLER has used this passus of WYDLER but has only forgotten to transcribe it into his usual notation; his diagram however does not support this supposition.

But even if EICHLER based his statement on his own direct observations, there is a probability that he was wrong on this occasion; a quite unusual situation indeed. Many years earlier, in 1837 the BRAVAIS brothers gave a description [1]) of the special inflorescence of *Statice*, based on extensive observations on 18 different species. They mention the remarkable fact that whereas the lower sterile bract in every member of the "cime unipare" is always well developed, the higher fertile bract aborts in many species; a relation which is probable unique. This result, which, according to my own observations on *Statice Limonium* seems to be right, has been overlooked by EICHLER. And as the calyx spiral on account of the open aestivation has to be derived from the prophyll positions, this may easily have spoiled EICHLER's results.

After all, there may still remain some doubt, as the special inflorescence of *Statice* and *Armeria* has never been fully understood until now. But in any case the exception of *Statice* to the general rule of heterotropic convolution becomes very doubtfull now, and the probability that *Statice* is no exception at all, is heightened still further by the fact that in the same family we have the genus *Plumbago* with heterotropic contort corolla and without any doubt the normal relation. WYDLER noted this (1856, l.c.) in two species, *Pl. Larpentae* and *Capensis*, not only from the position of the two prophylls, but also in terminal flowers from the preceding phyllotaxis of the bracts; I myself was able to confirm this in many flowers for both the same species.

We may therefore take it as very probable that the relation between calyx spiral and corolla convolution is always as BRAUN indicated, and that the reverse condition does not occur as a normal phenomenon in nature. We even find the normal relation in a flower that is not contort throughout, but only at the anterior side of the corolla, viz. that of *Tropaeolum maius*.

The corolla of this plant is commonly described as on the whole descendent, but with the difference that the median anterior petal is only half covered. CHATIN [2]) and ROHRBACH [3]) point to the fact that this last form of aestivation is identical with the contort one in four of the five edges; CHATIN calls it therefore subconvolutif, and ROHRBACH expressly states — what follows from CHATINs figures too — that it is "nach dem langen Weg", i.e. in this case the normal relation of BRAUN again.

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[1]) In their paper: Essai sur la disposition symétrique des inflorescences, Ann. d. sc. natur. Sec. Sér. Bot. T. **7**, 1837, on p, 312.

[2]) A. CHATIN, Mémoire sur la famille des Tropéolées, Ann. d. Sc. nat.; 4e Sér. Bot. T. **5**, 1856, p. 283.

[3]) P. ROHRBACH, Ueber den Blüthenbau von Tropaeolum, Bot. Zg. **27**, 1869, col. 833

EICHLER, who describes the aestivation as descendent [1]), gives a diagram with the reverse relation, petal 9 overlapping 6. This is however not what we find in the flowers; in accordance with CHATIN and ROHRBACH I found the condition of our fig. 3, without a single exception, in 25 flowers. We might describe this aestivation as descending in the posterior half and heterotropic contort in the anterior half.

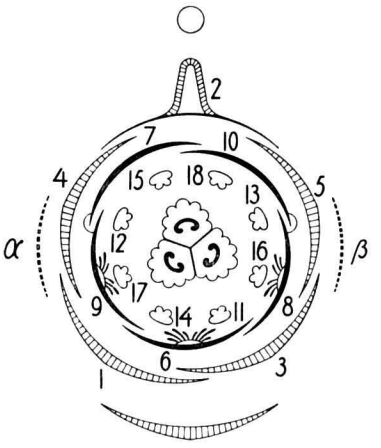

Fig. 3. Diagram of flower of Tropaeolum maius.

The petal numbering in our diagram is still born out by two further circumstances. The first is the observation of ROHRBACH [2]), that the dimensions of the petal primordia in the young flower point to a $^2/_5$ spiral origin, in the order of our numbering.

The second is that the petal spiral may be pursued in that of the stamens. The curious order in which the stamen primordia become visible, an order in which they shed their pollen too, has often puzzled botanists. It was however not accounted for till 1904, when CHURCH [3]) explained is as a normal Fibonacci spiral order, modified by unequal growth at the anterior and posterior side of the zygomorphic flower. The anterior stamens 11 and 14 are retarded, so that 11 is preceded by 12 and 13; the posterior stamens are somewhat accelerated so that 15 gets ahead of 14. Otherwise the order is not changed.

This normal spiral of CHURCH is the natural continuation of the petal spiral, as shown in our diagram.

Of course the fact that the relation between calyx spiral and corolla convolution is probably always the same, does not yet prove that our views on the cause of this relation are right. I have therefore tried to check these views in the following way.

In many species the corolla is not always fully contort, but a certain percentage of the flowers have deviations, show more or less variable imbricate aestivation. This has been stated more than once in literature [4]) and in my material such cases were to be found in great abundancy.

Now if the heterotropic convolution were merely the expression of the inner symmetry principle, we should expect these deviations, or faults as we may call them, to appear at random at the five edges of the corolla. If however the corolla is originally spiral, we may perhaps get more faults at the three edges, indicated by asterisks in our fig. 2. This must be the

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[1]) EICHLER, II, p. 297.

[2]) l. c. col. 835, Tab. 12, fig. 7.

[3]) A. H. CHURCH, On the relation of phyllotaxis to mechanical laws. London 1904; on p. 284—289.

[4]) e. g. EICHLER II, p. 112 and p. 277.

case when at the moment the petal margins come into mutual contact, the original differences in age and height of insertion are still present. But as aestivation notoriously arises only late in the bud, the differences between the petals may have disappeared as well when aestivation sets in; in that case the faults will be distributed at random.

My observations showed me, that both possibilities are realised in nature; I will here give three instances.

Plumbago Larpentae. Of 109 flowers 80 were contort; 29 showed one or more faults. Owing to a lack of technique in the beginning, I was only able to number the petals according to their position in 14 flowers.

These flowers showed the following faults: 6/8 (i.e. petal 6 overlapping 8) three times; 7/9 five times, 8/10 twice, 9/6 three times, 10/7 five times. If there had been any traces left of the spiral origin, the first three categories should have been more frequent than the last two; this was not the case. If we call 6/8, 7/9 and 8/10 rational faults, and 9/6 and 10/7 irrational, there were 10 rational and 8 irrational, whereas distribution at random on a total of 18 faults would give averages of 10.8 and 7.2.

Cistus polymorphus. Of 100 flowers 7 were partly tetramerous or hexamerous; of the 93 pentamerous flowers 71 were contort, 22 aberrant with altogether 28 faults. Of these 23 were rational, 5 irrational; chance would give as averages 16.8 and 11.2. The irrational faults were therefore not yet half as numerous as might be expected.

Geranium sanguineum. Of 100 flowers 8 had some open edge in the corolla. Of the remaining 92 only 25 were contort, 67 aberrant with a total of 103 faults. Of these 92 were rational, 11 irrational; chance would give as averages 61.8 and 41.2.

We thus see that the influence of the original spiral in *Plumbago* was absent, in *Cistus* discernible, but not very strong, in *Geranium* on the other hand preponderant.

SUMMARY.

The contort condition of the corolla of many plants is no proof of the whorled origin of the petals, but is due to a tendency to skewness in the individual petals.

In autotropic contort corollas the tendency is predetermined as to the direction of the skewness.

In heterotropic contort corollas the tendency is not determined as to the direction; the stimulus which brings the decision between right and left is given by the position of the adjoining sepals.

The constant relation between calyx and direction of corolla convolution is due to the fact that the petals are not laid down simultaneously, but in spiral order, the first petals determining with their skewness the convolution of the whole corolla.

Irregularities of the contort aestivation may be due to original differences in age and height of insertion according to the spiral origin of the corolla, when namely the differences have not yet been swept away by the whorl formation processes at the time aestivation sets in; in other cases the differences are no longer felt at the critical moment and then the distribution of the irregularities is governed by chance.