

OBSERVATIONS ON THE INFLORESCENCE IN THE  
FAMILY OF THE PLUMBAGINACEAE

by

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During a study of the corolla aestivation in Dicotyledons, the family of the *Plumbaginaceae* for several reasons struck my attention.

One of these reasons was the fact that the frequently contort corolla in some cases is autotropic, in others heterotropic <sup>1)</sup>, a combination which is rare in one and the same family.

Another reason was the fact that the statements in literature about the kind of contortion are uncertain and even sometimes contradictory. A most important controversy for my aestivation studies was that between the statements of Wydler (9, p. 39) and Eichler (3, I, p. 329) about the contortion of the genus *Statice*, which according to Wydler should be after the short way of phyllotaxis as in all other heterotropic corollas, according to Eichler after the long way which would be an unparalleled phenomenon in the plant world, putting serious difficulties in the way of an explanation of the heterotropic contortion in general.

Trying to solve some of the questions in hand by my own observations, I soon found that the inflorescence of the *Plumbaginaceae-Staticeae* is not only very interesting in a great number of special features, but that it is moreover very different in the different genera, and even sometimes in the species of the same genus; in the *Plumbaginaceae-Plumbagineae* on the other hand the inflorescence is much simpler and more easily understood.

A complete investigation of the important subject of the inflorescence and its forms in the whole family lying completely out of my reach for the present, I shall give here only some miscellaneous observations which would have been out of place in my paper on aestivation and which may perhaps induce someone to pay more attention to the curious features of the inflorescence in the present family.

<sup>1)</sup> For all questions of nomenclature compare Schoute (5).

I shall give these remarks in five paragraphs devoted to the genera *Plumbago*, *Plumbagella*, *Statice*, *Goniolimon* and *Armeria*.

§ 1. *Plumbago*. Eichler mentions about this genus (3, I, p. 328): "Die Blüten stehen.... in einfachen, durch eine Gipfelblüthe abgeschlossenen Köpfchen oder Aehren..... Vorblätter typisch 2 transversal.... steril ....Der zweite Kelchtheil gegen die Achse, doch bei *Plumbago Larpentae* finde ich ihn median nach vorn (Fig. 168 B)."

On these points I have to make the following remarks, based on an examination of *P. capensis* and *P. Larpentae*; for sake of convenience for the reader Eichler's diagram cited above has been reproduced in our Fig. 1.

The above description corresponds to the facts for *P. capensis*. The only additions I have to make are that the floral prophylls are

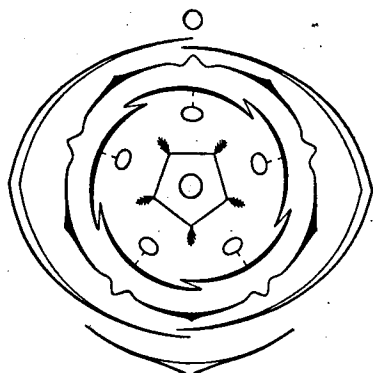


Fig. 1. Floral diagram of *Plumbago Larpentae* after Eichler, (3, I, p. 329).

rather strongly converging at the adaxial side,  $\alpha$  overlapping  $\beta$ , and that the calyx junction is sometimes a little different from that mentioned by Eichler, sep. 2 being slightly approached to  $\alpha$ , so that sep. 4 gets a transverse position.

For *P. Larpentae* we may make the following statements.

In the first place a point of minor importance: the bracteoles are not always sterile. Every terminal inflorescence has a large basal part where both the floral prophylls are fertile; this part is a transitional zone between the still lower part with the lateral branches, each ending in its own small inflorescence, and the higher part of the main axis where the flowers indeed have sterile prophylls. This transitional zone with its numerous dichasia, which is lacking in

*P. capensis*, forms an essential part of the inflorescence of *P. Larpentae*.

In the second place, and this is somewhat more important, the junction after the *Lobelia* mode, with sep. 2 at the front side as described by Eichler, does not occur; in reality the junction is as in the *Papilionaceae*, with sep. 1 at the front side.

This may be proved by the following facts. The prophylls are again rather strongly converging at the back side; a *Lobelia*-junction would therefore be already very improbable in itself.

Moreover we often meet with a slightly different junction, the unpaired anterior sepal being a little shifted towards  $\alpha$  so that the resulting calyx position becomes identical with that of the mentioned flowers of *P. capensis*.

A still more convincing argument may be derived from the last lateral sidebranches under the lateral dichasia, often small lateral sidebranches with a terminal flower and three bracts under the flower, each subtending a lateral flower. In this case the first and the second bract are not strictly lateral, but are approached at the adaxial side, the first overlapping the second one at the back side. The third prophyll is then placed at the front side, deviating from the median plane towards the first prophyll; in still lower lateral branches where we have four or more bracts, the normal spiral phyllotaxis begins in the same way.

In the dichasial and in the raceme parts of the inflorescence the two prophylls of the flower are placed in the same way, approached at the back side and  $\alpha$  overlapping  $\beta$ . There is therefore no doubt that the first sepal occupies the place which otherwise the third bract would have taken, the front side. That it is placed more or less accurately in the median plane instead of being shifted towards  $\alpha$  is a secondary complication; it is this which misled Eichler.

A last argument for the presence of a Papilionaceous mode of junction may be derived from the corolla aestivation, but to make that clear I have to go first into some detail about this aestivation.

The corolla has been described by Wydler (9) as heterotropic SW, i.e. that in a flower with a right calyx spiral the corolla is right contort. In the diagram of Fig. 1 the calyx spiral is, judged from the position of the prophylls when sep. 1 is at the anterior side, a left-hand one; the corolla is right contort. So the diagram gives another relation than the one described by Wydler.

As arguments for his statement Wydler mentions that he has observed terminal flowers of *P. capensis* and *P. Larpentae*, in which

the calyx spiral is the continuation of the bract spiral, so that this spiral can easily be determined. In lateral flowers he judged the calyx spiral from the prophylls, and found the same relation.

Both these observations were absolutely confirmed by my own observations; the lateral flowers in their adaxially approached prophylls furnished a reliable indication for a prediction of the direction of the corolla aestivation.

Eichler mentions for the genus *Plumbago* that he found the aestivation without any rule right or left contort, the right contortion being the most frequent. Notwithstanding the quite opposite results obtained by Wydler and myself, I believe that Eichler's statement will have been right: there may have been differences in the observed material, consisting either of other species or of other varieties. In that case the material observed by Eichler would have been a transition between anomotropic and right autotropic contort.

In *P. capensis* and *P. Larpentae* as observed by Wydler and by myself, there is however no doubt that the corolla is heterotropic SW in the terminal flowers and in the lateral flowers, but in the last mentioned ones only on the assumption of an „emprosthodromous” spiral, with sep. 1 at the front side. When we had the *Lobelia* mode of junction, and an opisthodromous spiral, the corolla aestivation should have been heterotropic SW in the terminal, and LW in the lateral flowers.

§ 2. **Plumbagella.** The inflorescence of *Plumbagella micrantha* is in many respects analogous to that of *Plumbago Larpentae*: in the racemes there is a basal part with lateral branches, similar to the main branch but smaller, and between these lateral branches and the higher single flowers there is a transitional zone where the bracts subtend 3-flowered dichasia.

Moreover the whole flowering part of the plant is of a sympodial construction. Every flowering branch forms about four foliage leaves and numerous bracts; from the first leaf an antidromous branch of the same character arises which is stronger than the apical part of its parent axis. The second, third and fourth leaf subtend similar but successively smaller branches.

The whole sympodium becomes more or less dorsiventral by the alternation of the spiral of the composing parts.

§ 3. **Statice.** The genus *Statice* has been divided by Pax into three subgenera with 13 sections. Anyone observing the conspicuous differences of the inflorescence in this genus would be inclined to expect the division to go still farther, even into distinct

genera. In any case a thorough description of the different types of inflorescence in the genus might furnish an interesting but comprehensive task for a monographer.

I shall confine myself here however to in many respects a very incomplete description of three types of inflorescence, that of *St. Limonium*, of a *St. sp.* cultivated under the wrong name of *St. echioides* and of *St. Suworowi*

1. *St. Limonium*. This type of inflorescence has also been met with in some other species, observed under several uncontrolled names which I shall omit here.

They have in common that there is a long and drooping main inflorescence axis, the basal part of which is radial and may have a spiral or a distichous phyllotaxis, the apical part being more or less dorsiventral and having a distichous arrangement of the inconspicuous bracts. These bracts subtend long distichous lateral branches, the first bract of which invariably falls on that side which corresponds with the physiological underside of the parent axis. The two orthostichies of their own bracts are also somewhat approached at the physiological underside, which for these branches is at the same time their abaxial side. The apices of these bracts and the branches springing from them are turned by a certain curvature to the physiological upperside.

The production of similar dorsiventral side branches may go on several times, especially in the lower part of the often large panicle; finally however instead of lateral branches partial inflorescences appear which may be called by the non-committal name of glomerules.

The use of this term may perhaps not be wholly appropriate, as the outer form of this conglomerate is not globose but rather spindle-shaped; the term has been used however for the same parts in *Armeria* by those most competent observers Ebel and Petri. Other authors use the term spikelets (De Candolle, Prodrômus) which is decidedly less appropriate. And as we shall see that the exact nature of the partial inflorescence may present some difficulties, the neutral name glomerule may be up to the mark.

The glomerules in *St. Limonium* (cf. Fig. 3) are somewhat flattened spindles, the right and left side being nearly flat. Their flowers are turned towards the sky. They are invested by two prophylls, a lower  $\alpha$  being placed, according to the rule for the bracts, at the physiological underside of the parent axis; its position is however not lateral on the glomerule but is shifted towards the adaxial side; in this way becoming intermediate between a lateral

prophyll of the Dicotyledons and an adaxial prophyll of the Monocotyledons.

The  $\alpha$ -prophyll is amplexing and has a conspicuous green midrib, protruding with a red point; the remaining part is scarios and very unequal-sided, the adaxial lobe being much larger than the other.

The  $\beta$ -prophyll is clearly overlapped by the  $\alpha$ ; it is opposed to it and therefore shifted to the bract side. It is much larger and of a firm texture.

This  $\beta$ -prophyll encloses a row of 1 — 5 flowers, or even more, the eldest being placed before  $\alpha$ , the youngest which, as Ebel reports (2, p. 13) often does not reach the anthesis, at the side of  $\beta$ .

This glomerule has been described by the Bravais brothers (1, p. 312) as a "cime unipare distique"; from their statements and figures, reproduced as our Fig. 2, we may summarize their descrip-

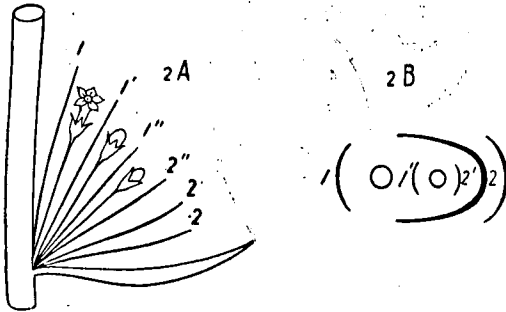


Fig. 2. A, Longitudinal diagram of glomerule of *Statice*; B, transverse diagram of same of *St. Tripteris* and *St. Limonium*, after the Bravais brothers (1, Pl. 10. Fig. 28 and 28bis).

tion in our own terms as follows: a sickle with two bracts (1 and 2, 1' and 2', etc.) in the median plane for every flower, the lower 1 or  $\alpha$  being always sterile, the higher 2 or  $\beta$  being fertile; in many species the higher fertile prophylls disappear by abortion. The position of  $\alpha$  and  $\beta$  is not always strictly median; on the contrary the number of species with median prophylls is very small; in the majority of species  $\alpha$  is shifted "vers l'horizon" which may probably mean to the physiological underside; in other species it is shifted towards the sky.

Most authors however call these glomerules cincinni (Eichler 3, I, p. 328; Pax in Engler & Prantl) and as we shall see

on good arguments. The flowers are namely, as has been represented in Fig. 3, placed in two rows, at least in the *Limonium*-type, and their well-developed  $\alpha$ -prophylls show by the position of their midribs that the flowers alternate in the direction of their spiral.

Moreover, the contortion of the corollas, if present, alternates in the successive flowers of every glomerule; in *Limonium* there is consequently hardly any doubt left: the glomerule is a cincinnus with furthering from  $\beta$ . We shall see however that in other species the conditions may be rather uncertain.

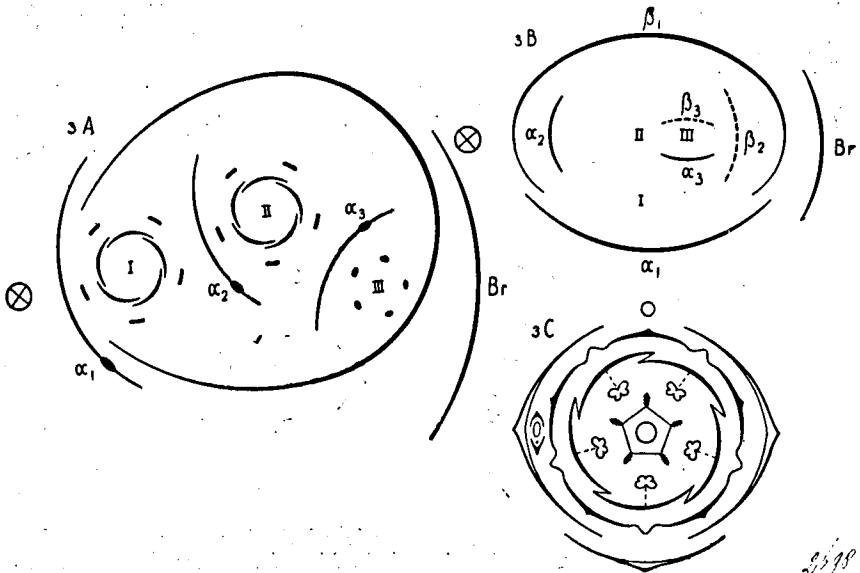


Fig. 3. A, *Statice Limonium*. Diagram of right glomerule; B, same with theoretical rearrangement of floral prophylls; C, *Statice latifolia*, diagram of glomerule after Eichler (3, I, p. 329).

For a more detailed description I give a diagram of a „right” glomerule; a glomerule being called right here when it has to be drawn in the usual orientation of a diagram on the right side. In the living object these right glomerules are on our right hand when we hold their parent axis with its flowers up and the apex towards us.

In the diagram 3A we see that the main flower I has a sepal towards the axis, as far as this may be stated in a complex with so many bends, turns and shifts; the second flower II is placed

before the opposed petal and also turns again a sepal towards I. The third flower III, however, is not placed before the opposed petal, but before another petal; the junction of III to II is the same as that of II to I and the higher flowers if present all continue in the same way.

All  $\alpha$ 's being developed, the  $\beta$ 's all abort from  $\beta_2$  onwards; I never saw any trace of them in my material.

The corolla of I is nearly always contort, in a right glomerule left, in a left one right contort: out of 203 flowers I of *Limonium* there were 2 quincuncial, 14 vicinal, 1 distal and 186 contort, all after the indicated direction.

Flower II on the other hand is usually much more variably imbricate: out of 110 flowers II there were 16 quincuncial, 27 vicinal, 44 distal and only 23 contort; these 23 were however without exception right contort in right glomerules and left in left. In Fig. 3A flower II has therefore been represented as right contort; in other species with the *Limonium*-type of inflorescence and more-flowered glomerules the flowers II and IV as a rule were right contort in right glomerules, the flowers I, III and V left contort.

For determining the kind of contortion it is not sufficient to know that the successive flowers alternate in their contortion direction, we ought to know moreover the relation between calyx spiral and contortion direction. The calyx however does not betray its spiral in any way in the older bud or in the expanded flower. A quincuncial order of development is mentioned by Payer for *Armeria* and *Plumbago*, and probably occurs here too; a developmental study should confirm this and determine the direction of this spiral.

Such a study being wanting we may remark that if the mode of calyx junction is the usual one of most Dicotyledons, a mode which also occurs in *Plumbago*, with sep. 2 towards the parent axis, the contortion is of the usual heterotropic kind, after the short way of phyllotaxis.

As mentioned above this is what had been stated by Wydler, but it militates against the statement of Eichler, confer Schoute (5). It is however not difficult to prove that the diagram given by Eichler in confirmation of his statement, which has been reproduced in our Fig. 3 C is wrong, and that it must have been drawn after the text and not from nature.

To understand this we have to recast our diagram and to bring it into the theoretical form in which the prophyls are strictly



lateral and no shifts occur; confer Fig. 3 B. It is now comparable with Eichler's diagram, 3 C. As we see from the configuration of the represented flowers, Eichler's diagram is that of a left glomerule. Now a left contort corolla as drawn by Eichler never occurs, as far as my experience runs, in the first flower of a left glomerule, neither in *St. Limonium* nor in *St. latifolia*; the species drawn by Eichler, nor in any other species of this group.

We have now still to compare Fig. 3 B with 3 A, to get an impression of the different shifts which presumably must have taken place during development. Of course one may maintain that perhaps no shifts occur at all but that all parts are laid down in the position they are to occupy in the adult condition. But the quite unusual positions which are different in the different *Statice* groups, and the strongly dorsiventral character with the many bends and turns make the former view the more probable.

Flower I has two developed and opposed prophylls; the natural supposition is therefore that I has been turned with its prophylls through more than  $45^\circ$  and less than  $90^\circ$ , in such a direction that  $\alpha$  approaches the parent axis and  $\beta$  the bract.

Flower II has only an  $\alpha$  developed; the position of its  $\beta$  is revealed by the presence of III. These two prophylls are not opposed but about at right angles to each other; we may suppose that they are approached to each other on the adaxial side, and that together they are turned, with II, in the opposite direction through somewhat less than  $90^\circ$ .

Flower III and, if present, the following flowers show similar conditions. The difference between the shift of  $\alpha_1$  and the following  $\alpha$ 's is demonstrated by the curious fact that the midribs of the second, third and following  $\alpha$  are placed at the right and the left alternately, but that the  $\alpha_1$  and the  $\alpha_2$  seemingly lie on the same side.

2. *Statice* Sp. One culture gave one single inflorescence which was studied. A nearer investigation remaining desirable in several respects, the main conditions may be mentioned here.

The flowers of the inflorescence were not turned towards the sky, but towards the earth, so that in a detached part of the inflorescence the under side would be taken for the upperside. This may correspond to the statement of the Bravais brothers that: "Les fleurs se déjettent d'un même côté, ordinairement vers le ciel, quelquefois vers l'horizon".

Keeping a branch in the natural position, the flowers on the underside and the apex towards us, the diagram of a right glomerule may be represented by Fig. 4 A, and Fig. 4 B may again

represent the same under the supposition that all prophylls were exactly lateral.

We see that  $\alpha_1$  here lies on the side of the bract and somewhat on the upper side,  $\beta_1$  on the axis side, somewhat towards the underside, in exactly the reverse positions therefore from that in *St. Limonium*. This may be attributed to a turning of prophylls and flower I through more than  $90^\circ$  in the opposite direction from that in *Limonium*.

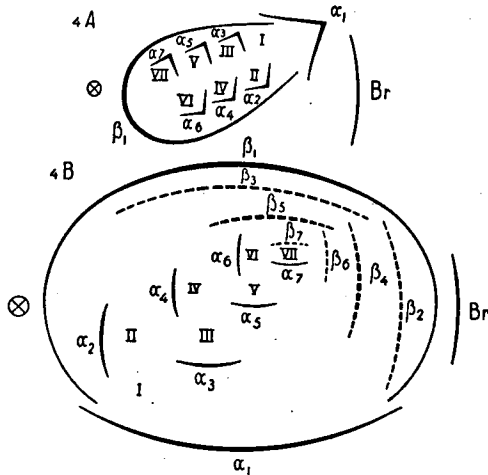


Fig. 4. *Statice Sp. A*, diagram of right glomerule; B, same with theoretical rearrangement of floral prophylls.

A shorter turn, through less than  $90^\circ$  might equally well reduce both prophylls to a lateral position,  $\alpha_1$  on the upper and  $\beta_1$  on the under side. But as without any doubt flowers II, IV and VI have their  $\alpha$ -prophyll on their right, and III, V and VII on their left, we have to expect that I will have its  $\alpha_1$  on its left also; and further if  $\alpha_1$  originally stood on the right, the flowers I and II would be homodromous.

The diagram Fig. 4 B on the other hand, which has been derived from 4 A only by application of the ordinary rules for the construction of diagrams, is identical to our Fig. 3 B for *St. Limonium*, a result which surely is to be taken as a confirmation of its correctness.

The corolla aestivation, being only observed in a few flowers which were variably imbricate, did not furnish a clue for the determination of the calyx spiral or the mode of junction.

3. *Statice Suworowi*. In this species the inflorescence is an

erect and radial spike of glomerules, the glomerules being inserted on the main axis in a normal spiral.

Every glomerule has a subtending bract (Fig. 5 A) and one single large secondary bract in the median plane right over the subtending bract. There are further mostly three flowers in a single median row, over the two bracts, in a descending serial order.

This glomerule therefore differs greatly from the preceding forms and it has been described by Velenovsky as a sickle (8, p. 799, Fig. 490 II and p. 833). The description of the Bravais brothers of the glomerule of *Statice* in general as a sickle may

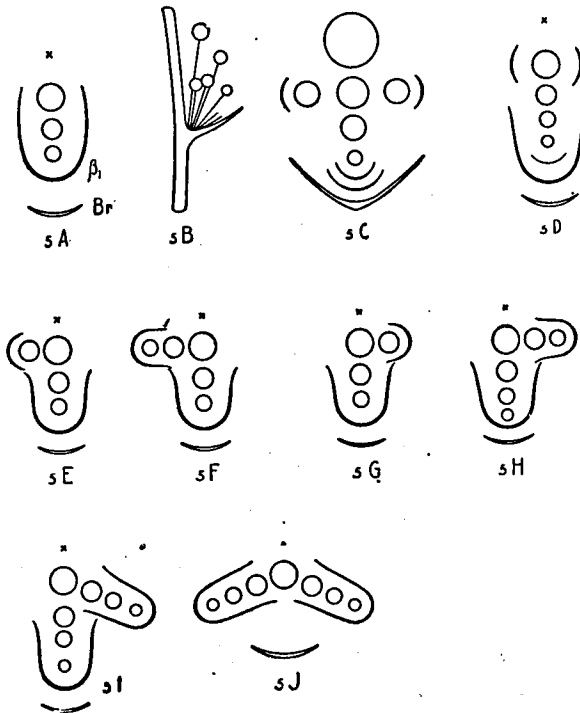


Fig. 5. *Statice Suworowi*. A, diagram of normal glomerule; B and C vertical and transverse diagrams after Velenovsky (8, p. 799, Fig. 490 II); D - J diagrams of transitional forms between the highest lateral inflorescences and the lowest glomerules.

have been based on this or similar forms. Indeed the glomerule has all the properties of a sickle and it is the occurrence of such forms which necessitates the use of a neutral term such as that of glomerule for the partial inflorescence of the genus.

A third description has been given by Schumann (6, p. 339), but though even the developmental history has been traced, his rationalistic views prevent him from observing any morphologically important relations. His conclusion that the glomerule consists of a row of descending serial flowers, subtended by two superposed bracts and without any developed or aborted floral prophylls, but that if somebody should decidedly want to suppose a genetic relation between the flowers, he might also class the glomerule as a sickle, needs no further consideration.

Velenovsky mentions moreover the existence of some additional prophylls; his figures are therefore reproduced here as  $\zeta$  B and  $\zeta$  C. Beyond the normal secondary bract indicated by him as  $\gamma$ , he observed in the lowermost glomerules a third median anterior bract  $\alpha_1$  and two lateral bracts  $\alpha$  and  $\beta$  for the main flower.

In the material of the Groningen Botanic Garden all glomerules normally only had the diagram  $\zeta$  A, every flower with one sepal towards the main inflorescence axis and without the slightest zigzag in the flower row.

Under every terminal inflorescence there were however several smaller similar lateral inflorescences, unessential branches in the terminology of Braun, and between the highest of these lateral inflorescences and the lowest glomerules of the main axis intermediate formations sometimes might be observed. Of these I observed the cases D—J; D being like the one figured by Velenovsky, E—J giving other aspects.

The comparison of these different cases with the diagrams of the preceding forms of *Statice* brings me to the following views on the facts.

The glomerule of *Suworowi* really is a sickle, but at the same time it is nothing but a mere variation of the cincinnus of *Limonium*. It is of the same type, i.e. with furthering from  $\beta$ . Its  $\alpha$ -prophylls always abort, so that their position cannot be determined exactly; the  $\beta$ -prophylls with the exception of  $\beta_1$  also abort. All these  $\beta$ -prophylls whether aborted or not, are placed exactly in the median plane, abaxially, in the position described by the Bravais brothers as characteristic for the genus *Statice*.

In some cases a  $\beta_2$  may appear; further, in transitional forms between lateral inflorescences and glomerules there may be occasionally two lateral bracts, the first phyllomes of the shoot, having the plastics of bracts, not of an  $\alpha$ -prophyll (aborted) nor of a  $\beta$ -prophyll. These bracts may be sterile ( $\zeta$  D) or they may subtend glomerules of the ordinary description (E—I). Between

them there may be a third bract with a large glomerule (C, D) or it may be lacking (J).

In other cases there may be a single lateral bract (E—I); in such cases there is one large median glomerule about which it is uncertain whether it owes its origin to the second phyllome of the shoot, shifted to the median plane, or to the third, the second having aborted.

The corolla aestivation being autotropic, right contort, does not furnish additional information about the inflorescence.

§ 4. *Goniolimon*. My material consisted of two cultures of *G. tataricum* and one of *G. tataricum*  $\beta$  *angustifolium*, a variety with one-flowered glomerules.

The inflorescence in *Goniolimon* is essentially of the type of that of *St. Limonium*. The branches bear distichous bracts which are inserted somewhat towards the physiological under side of the axis, though the bracts themselves and the glomerules are bent towards the upper side.

Every glomerule has an  $\alpha$ -prophyll whose base overlaps at both sides the large and trifid  $\beta$ -prophyll. The position of these prophylls is such that the  $\alpha$ 's lie on the physiological underside, the  $\beta$ 's on the upperside. They may be strictly lateral, usually however they are somewhat shifted,  $\alpha$  towards the bract,  $\beta$  towards the axis, though the reverse shift may also occur to a slight extent.

Two-flowered glomerules are the rule, three-flowered are only to be observed in the basal parts of the glomerule bearing axes. In these three-flowered glomerules the zigzag is very clear and the arrangement is that of Fig. 6 A. This recalls our *Statice* sp., the only difference being a less extensive torsion, but in the same direction.

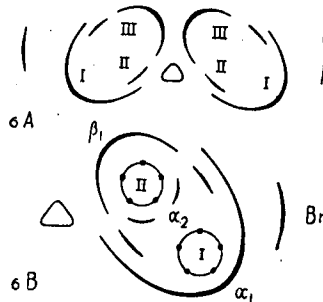


Fig. 6. *Goniolimon tataricum*. A, diagram of inflorescence axis with two three-flowered glomerules; B, diagram of right glomerule.

Fig. 6 B represents a diagram of a two-flowered glomerule. The only notable difference from the glomerule of *Statice Limonium*, when we disregard the different orientation, is the presence of two narrow bracts in the place of the sterile  $\alpha_2$ ; we find here two long scarious strips of similar habit. Of course we might think to find in them the two prophylls of flower II, approached at the adaxial side; this natural supposition was however not to be corroborated in any way and meets with the serious difficulty that the  $\beta_2$  would be strongly shifted whilst its axillary bud flower III would not be, or might even be shifted in the opposite direction. Therefore I prefer to take these two strips simply as one single but deeply bifid  $\alpha_2$ .

The corolla is contort in many cases, in other cases variably imbricate. Of course one would expect that the contort corollas of the first flowers of right glomerules would be left contort and reversely; not only from the analogy with *St. Limonium*, but also because the position of  $\alpha_1$  and  $\beta_1$  imply that in the case of an emprostnodromous calyx spiral the heterotropic corolla should be so.

To my great surprise the expectation was only partly fulfilled, as the following table will make clear.

Corolla aestivation	First flower of glomerule on the			
	left side		right side	
	<i>G. tataricum</i>	<i><math>\beta</math> angustifolium</i>	<i>G. tataricum</i>	<i><math>\beta</math> angustifolium</i>
right contort	20	18	7	3
right vicinal	7	1	2	1
left contort	7	8	27	16
left vicinal	5	0	9	1
quincuncial	2	0	3	1
distal	4	1	7	0
	<u>45</u>	<u>28</u>	<u>55</u>	<u>22</u>

As we see the number of contort SW preponderates every where; in *tataricum* it is 47 in 100 flowers, in the variety *angustifolium* it is 34 in 50, far removed from any chance distribution.

Thus it would be alright but for the abnormal percentage of the reverse contort condition, being 14 in the 100 and 11 in the 50 flowers, a percentage that is too far removed from any chance, as in 100 flowers with variably imbricate aestivation the chance of contort LW only is  $3.1 \pm 1.2$  cases.

It was this puzzling result that brought me to the conviction that there must be a third kind of contort aestivation, which I

have termed anomotropic, where the direction of the contortion is variable as in the heterotropic form, but where the determination is not connected with the calyx spiral but entirely depends on chance.

In *Goniolimon* this anomotropic aestivation is not met with in a pure form, the calyx spiral still having a great influence; we must therefore say that the present case represents a mixture of heterotropy and anomotropy, just as in *Plumbago* there may probably sometimes be a mixture of anomotropy and autotropy.

As mentioned above, in *Goniolimon* the two-flowered glomerules are the rule. A number of flowers II were also examined; here the aestivation was variably imbricate and contortion absent: this is again a remarkable parallel of a quite unexplained phenomenon in *Statice Limonium*.

§ 5. *Armeria*. The inflorescence of *Armeria* has the form as every body knows of a head. On closer examination its construction is rather complicated. The best description in literature <sup>1)</sup> is surely that given by Petri (4, p. 26).

According to Petri the head is composed of a number of glomera, each consisting of a transverse row of glomerules, the glomera being screws and the glomerules cincinni. This statement has been copied by Eichler; a full diagram of such a glomus has not been published as far as I know.

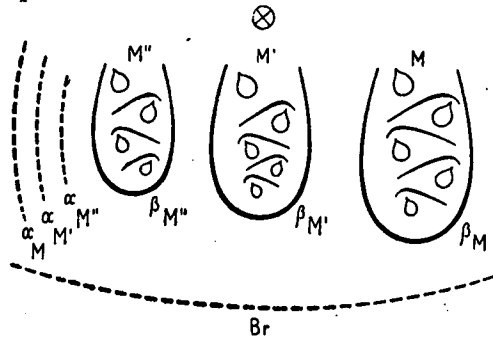


Fig. 7. *Armeria* spp. Diagram of glomus from head with right-hand involucre spiral, with three glomerules.

I shall begin therefore by giving such a diagram, Fig. 7, after my observation on several cultures of undetermined *Armeriae* spp.

The subtending bracts Br of the glomera are placed on the

<sup>1)</sup> The description given by Schumann (7, p. 550) gives a new proof of the impotence to which the rationalistic school of Hofmeister may lead in morphology.

top of the peduncle of the head in a normal spiral, in the continuation of the spiral of the involucre bracts. The subtending bracts themselves are either all wholly aborted, as Petri contends to be the case in all species, or a number of the outer glomera have well-developed bracts, with the form and properties of involucre bracts. This last condition I met with in an *Armeria* under the name *A. setacea*, where only 4 or 5 involucre bracts were sterile, and the bracts number 5 or 6 up to number 15 to 17 subtended well-developed glomera, only a very few inner glomera being subtended by aborted bracts.

Every glomus consists of 1 to 5 glomerules of different ages. The oldest glomerule of every glomus is situated in heads with a right-hand involucre spiral at the right, as Petri already mentions. The glomus has no secondary bracts of any kind; discussion of its character will therefore better be postponed until the glomerule has been treated.

Every glomerule is enveloped by a stout secondary bract,  $\beta$  of the diagram, inside which the double row of flowers is to be found. The first and oldest flower of the glomerule, M, is placed towards the centre of the head, on a short pedicel at the head of that one of the two flower rows which is nearest to the younger glomerules. The insertion of the flower on the pedicel is such that the limiting plane between pedicel and flower is an oblique one. The position of the lowest point of this slope has been indicated in the diagram by a point in the outline; one of the five sepal nerves abuts on this point, which in the living object remarkably reminds one of a tiny calyx spur.

The second flower is placed at the head of the other flower row; it is covered on the adaxial side by a scarious prophyll, like all further flowers of the glomerule. Its „calyx spur” is placed in the same way as in I, but somewhat to the opposite side. All further flowers show the same conditions in a continuously alternating order.

The above description will make clear that Petri is right in declaring the glomerule to be a cincinnus; a further argument given by Petri is the alternation of the corolla contortion direction in the successive flowers of the glomerule.

Petri gives moreover an obvious explanation for the remarkable fact that the main flower is not, like all other flowers of the cincinnus, provided with an adaxial secondary prophyll: the prophyll  $\alpha$  which ought to have been present on the adaxial side of the main flower has been shifted to a lateral position in which it has produced the next glomerule in its axil, having



itself suffered abortion like the subtending bract of the glomus.

From the above the whole construction of the glomus may be elucidated. The first flower of the first glomerule is the axillary product of the subtending bract Br; in the diagram it has therefore been indicated as M, main flower.

Both prophylls of this M have produced a flower; the well-developed  $\beta_m$  has given the antidromous second flower of the first glomerule; the aborted  $\alpha_m$  has produced the homodromous main flower M' of the second glomerule, all according to the general rules for so many dichasia.

We see therefore that the glomus is a sickle of homodromous flowers from  $\alpha_m$ ,  $\alpha_m'$ ,  $\alpha_m''$  etc; each of these flowers gives rise to a cincinnus from its  $\beta_m$ . The whole inflorescence in this way must be a head of sickles of cincinni.

In the description of Petri which is on the whole correct, there is one wrong element: the third flower is taken as an axillary product of the developed prophyll of the second flower and so on.

As may be seen from our diagram this cannot be true: the developed prophyll of flower II being placed opposite flower III cannot be its subtending bract, but flower III must be the axillary product of an aborted second prophyll of flower II.

The comparison with *Statice* confirms this the more; the developed prophyll of flower II is its  $\alpha$  and the aborted one its  $\beta$ .

As we described above the glomus as a sickle and Petri called it a screw, this might be taken as different interpretations of the facts; we have however to bear in mind that at the time of Petri's dissertation the conception of the fan and the sickle as types of monochasia had not yet been published by Buchenau, and that the only division of the monochasia was that of Schimper and Braun in cincinni and screws, the former being characterized by antidromous, the second by homodromous flowers. From this point of view the glomus with its homodromous flowers undoubtedly belongs to the screws.

It is however out of doubt that the inclusion of the glomus with its single row of main flowers amongst the screws may have strongly contributed to the origin of misunderstandings; in fact Eichler and all later botanists with him have been induced to more or less grave mistakes, one of which was that the supposed screw was attributed not only to *Armeria* but also to *Statice* and other *Staticeae*.

As to the corolla aestivation, the different species apparently are different. Petri and Döll find it to be alternately right and left contort in the successive flowers of the glomerule. Eich-

ler on the other hand finds it to be constantly right contort in all flowers, and this was my experience too.

Obviously both kinds of contortion, the heterotropic and the autotropic, occur in different *Armeriae* spp. Having seen no species with a heterotropic corolla myself, I have not been able to check the very probable supposition that it is contort SW, or left contort for the flowers of the left rows and right contort for the right rows.

### SUMMARY.

1. Some points of the inflorescence in the genera *Plumbago*, *Plumbagella*, *Statice*, *Goniolimon* and *Armeria* are described.
2. In *Plumbago* and *Plumbagella* the inflorescence, though being of the racemose type, may have a certain basal part in which lateral three-flowered dichasia are produced (*Plumbago Larpentae*, *Plumbagella micrantha*).
3. In *Plumbago* the usual calyx junction with sep. 2 towards the axis may occur (*Pl. capensis*), or the Papilionaceous junction with sep. 1 towards the bract (*Larpentae*). The *Lobelia* junction, described by Eichler, does not occur.
4. The corolla aestivation in *Plumbago capensis* and *Pl. Larpentae* is heterotropic in the usual form of contort SW. In some species or varieties it is probable that the aestivation may be a transitional form between the right autotropic and the anomotropic form.
5. The inflorescence of *Statice* may show many variations; the ultimate endings, the so-called glomerules are of a rather constant construction.
6. These glomerules are monochasia from  $\beta$ ; they may be cincinni (*Limonium*, *St. Sp.*) or sickles (*Suworowi*).
7. The  $\alpha_1$ -prophyll of the *Statice* glomerule may shift from the lateral position towards the axis (*Limonium*) or towards the bract (*St. Sp.*); in *Suworowi* its place is made uncertain by its abortion.

The  $\beta_1$  prophyll is opposed to the  $\alpha_1$ .

The higher  $\alpha$ -prophylls are either developed (*Limonium*, *St. Sp.*) or aborted (*Suworowi*); they may be approached adaxially towards the  $\beta$ -prophylls, even so much so as to become situated at the opposite side of the flower (*Limonium*) or they may remain in their lateral place (*St. Sp.*).

The position of the higher  $\beta$ -prophylls may be lateral (*St. Sp.*) or somewhat shifted to the abaxial side (*Limonium*), or they

- may lie adaxially in the median plane (*Suworowi*).
8. The flowers of *St. Limonium* and *St. Sp.* have an emprosthe-dromous calyx spiral.
  9. The *Statice* corolla is often contort; this may be heterotropic SW (*Limonium*) or right autotropic (*Suworowi*).
  10. The inflorescence of *Goniolimon* is much like that of *Statice Limonium*; the glomerule is built in the same way, only with a trifid  $\beta_1$ , and a deeply bifid  $\alpha_2$ .
  11. The corolla aestivation in *Goniolimon* for flower I is inter-mediate between heterotropic contort SW and anomotropic; for flower II it is variably imbricate.
  12. The inflorescence of the genus *Armeria* is a head of glomera (sickles from  $\alpha$ ) of glomerules (cincinnati from  $\beta$ ).
  13. The fertile bracts of *Armeria* all abort, with the exception of some of the external glomus bracts and of all  $\beta_1$ -bracts of the glomeruli. The sterile bracts all develop.
  14. The corolla aestivation of *Armeria* is either right autotropic or heterotropic, probably SW.

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