ON THE AESTIVATION IN THE CYATHIUM OF EUPHORBIA FULGENS, WITH SOME REMARKS ON THE MORPHOLOGICAL INTERPRETATION OF THE CYATHIUM IN GENERAL

by

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Dedicated to the memory
of A. W. EICHLER († March
2nd 1887, at the age of
47) on the fiftieth anni-
versary of his death.

Contents.

Introduction.

In the course of a study of the corolla aestivation of Dicotyledons I was obliged some time ago to make a comparison of the contort corolla with the contort appendages of *Euphorbia fulgens* (10, p. 44); the aestivation of these appendages proved to be heterotropic, i.e. changing in direction with the phyllotactical spiral, and moreover SW (= short way) heterotropic, i.e. a right hand spiral is accompanied by a right contortion and reversely.

As a detailed study of this aestivation seemed promising, the observations were continued, with the aim of checking the correctness of the views already given on the origin of heterotropic contortion. This was the more attractive as the preliminary observations already suggested that the involucre itself should be heterotropic contort too, a fact which was soon confirmed on further observation.

These observations giving support to the classical interpretation of the involucre and the glands, which had been doubted by some recent authors, a second chapter on the morphological interpretation of the cyathium may follow.

Chapter I. Euphorbia fulgens.

Some knowledge of the inflorescence being required for the study of the relation between phyllotactical spiral and aestivation, the present chapter will begin with a paragraph on the inflorescence.

§ 1. The inflorescence.

The inflorescence of *Euphorbia fulgens* may be characterized as being a terminal compound raceme, ending in cincinni of cyathia.

The main axis of the plant consists of a long vegetative part with large foliage leaves, occasionally subtending similar lateral leafy axes, and a terminal flowering part with similar foliage leaves, subtending lateral branches with small red deciduous bracts, but no foliage leaves.

Towards the apex of the main axis the foliage leaves rapidly diminish in size, and they may be followed by some small bracts like those of the lateral branches. At the apex a terminal cyathium is sometimes present; in the majority of cases however the last part of the main axis aborts [1]).

The lateral axes are better developed repetitions of the apical part of the main axis, the lower ones bearing under their terminal cyathium about six bracts, the higher ones a gradually diminishing number of 4, 3 or rarely even only 2 bracts [2]).

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[1]) EICHLER writes (1, p. 302) that the main axis of *E. fulgens* is unlimited; this statement is not quite correct.

[2]) The distribution of these bracts shows the following remarkable, but unexplained, feature. The lower lateral branches with four and more bracts begin with a very small basal α-prophyll, sometimes subtending a small bud. The β-prophyll is much larger, having the same dimensions as the following bracts which will be called here γ—ζ. This β is opposed to α, but inserted some mm higher up. The next bract, γ, may be superposed to α, or it may be placed like δ—ζ in a common spiral arrangement, and then it falls on the abaxial side; in any case δ falls on the adaxial side.

The lower bracts of the lateral branches being sterile, only the higher bracts are fertile; in the lower lateral branches there may be three, in the higher two or finally only one fertile bract.

These fertile bracts subtend cincinni of cyathia, every cyathium peduncle bearing two bracts of which the second is fertile.

The phyllotactical spiral of the lateral branches is often antidromous to that of the main axis (in 100 lateral branches 70 were antidromous, 30 homodromous); the first member of the cincinni is often homodromous to its parent axis, whereas the following cincinnus members are always antidromous.

§ 2. The aestivation of the appendages.

The earlier result that the contortion of the appendages is SW heterotropic was confirmed in the numerous continued observations in all cases. It is so in the cyathia terminal to the main axes, when developed; here it is connected to the phyllo-

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When tracing the spiral of the higher bracts downward, we always find that it runs between α and β on the adaxial side, opisthodromously. Consequently we have the simple relation that a branch with its α on its right has a right contort appendage whorl in its terminal cyathium.

In the higher lateral branches of the main axis we find not only that the number of bracts decreases, but moreover we see that the α-prophyll, remaining at its basal insertion level, gradually diminishes in size and finally disappears.

Yet the phyllotaxis and the contortion of the appendages remain the same; so that a lateral branch without basal bract, and with its first bract at some mm from its base on its left, has a terminal cyathium with right contort appendages.

We can therefore hardly avoid the conclusion that the α-prophyll in such cases has wholly aborted. Once this is granted, we are led to the further conclusion that in the cincinnus members the two well developed bracts are not α and β, but β and γ, as they are inserted at the same higher level, and a member with its first visible prophyll on its left has right contort appendages. And this is corroborated by the fact that the first involucral bract is situated at the adaxial side, in the position of δ.

To these views in themselves there is little to be objected. But we have to bear in mind that the peculiar position of the first involucral bract on the adaxial side which is in contrast with the condition usually found in calyces, is almost general in the genus *Euphorbia* (Wydler, 8, p. 433, footnote 3 writes that some species, which he does not enumerate, make exception; Schmidt, 12, p. 32 describes *E. splendens* as such an exception), and that therefore the conclusion of an aborted α-prophyll logically should be extended over the whole genus or over most of its species. Of course this is not to be accepted without further research.

If it should be confirmed, the cyathium would be brought still more in line with lateral flowers; namely in both the phyllotactical spiral would run opisthodromously from (the aborted) α to β.

tactical spiral of the foliage leaves. It is moreover the case in the terminal cyathia of the lateral branches and in the cincinnus cyathia. In the latter two categories the position of the first prophyll, as remarked in footnote 2 above, permits one to predict the contortion direction.

In a small minority of cases the aestivation, instead of being contort, is vicinal (= cochlear, the overlapping being next to the overlapped appendage, see SCHOUTE, 10, p. 24) or distal (= cochlear, the overlapping and the overlapped appendage not being neighbours). These cases were studied in detail, as they might be of interest for the theoretical explanation of the contortion.

Our fig. 1 represents a diagram of the main axis of a lateral branch with its terminal cyathium; the appendages in the latter have been indicated by the letters *a*—*e*, in the same way as before (10, p. 45). Now I moved earlier, that the appendage *a*, being the commissural product of the involucral bracts 1 and 3, might be the first to be initiated and that the other appendages might be laid down in the order indicated by the letters. This supposition is corroborated now by the newly observed facts in the following way.

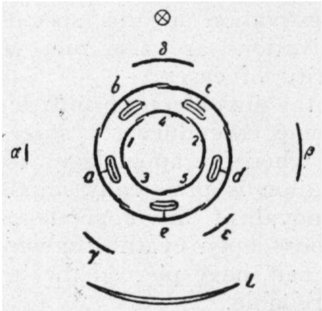

FIG. 1. Euphorbia fulgens. Diagram of lateral branch of inflorescence. L subtending foliage leaf, α—ε bracts, 1—5 involucre of cyathium, *a*—*e* petaloid appendages. The cincinni of cyathia from δ and ε, the cincinni of male flowers from 1—5 and the terminal female flower have been omitted.

In 25 cyathia with abnormal aestivation (24 vicinal, 1 distal) the position the appendages occupied with respect to the bract spiral was determined, or in other words the appendages were classified as *a*, *b*, *c*, *d* and *e* appendages.

In all 24 cases of vicinal aestivation four of the edges showed the normal contortion direction, only one edge being abnormal. In 17 of these cases it was *a* that instead of being covered by *e*, was overlapping *e*, in 5 cases *b* overlapped *a*, in one case each *c* and *d* were wholly overlapping. In the distal case three edges were normal; here *a* overlapped *e*, and *e* in its turn overlapped *d*.

So these deviations evidently were only incidental changes of the normal contortion, but their distribution strongly supports the idea that *a* is laid down first, and then *b*.

§ 3. The aestivation of the involucre.

As far as I know an aestivation of the involucre has never been described in a *Euphorbia*. Only Troll gives a drawing of a cyathium of *Euphorbia fulgens* (13, p. 162, fig. 111), in which the involucre is contort. And indeed contortion is the most common involucre aestivation in this species, though cochlear and quincuncial aestivations are also met with often, even in a rather great minority of cases.

The aestivation of the involucre is only to be observed with certainty and with some ease during a stage of short duration. In the bud condition, when the appendages are still covering the involucre, the observation is practically impossible in the living state, as by the removal of the appendages the latex floods everything. And in those open cyathia in which the gynoecium, or more than one stamen, have pierced the involucre, the observation is no longer reliable.

In the later formed cyathia which are mainly female [3]), the gynoecium piercing the involucre even before the appendages expand, all observation becomes impossible; the male cyathia of the early flowering period on the other hand present a suitable material for the observation, in great numbers.

In the drawing by Troll the contortion direction of appendages and involucre is the same. This condition was never met with in my material, the two whorls always being contort in different senses as represented in fig. 1. Indeed we may state that the involucre is LW heterotropic.

The theoretical importance of this fact will be discussed in the next paragraph, here the description of some non-contort cases may follow.

Out of 25 selected cyathia with a different aestivation 17 were

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[3]) The successively developed cyathia show a sexual differentiation, as mentioned already by Roeper (9, p. 38) for the German spp., and by Goebel (4, p. 198) for *E. fulgens* in particular.

vicinal, 8 quincuncial. By determining the bract spiral the involucral bracts were numbered, and the results were as follows. In the 17 vicinal involucres four edges were LW heterotropic in each; the aberrant edge was 15 times 1/4 (= bract 1 overlapping 4) and 2 times 2/5. In 7 of the 8 quincuncial involucres there were two deviations from LW heterotropic, namely invariably 1/4 and 2/5 so that the aestivation became eutopic throughout. In the eighth cyathium there were three deviations, 1/4, 2/5 and 5/3. Out of 34 deviations 33 were therefore returns from the contort to the eutopic aestivation, only one deviation being an "irrational fault".

This result surely again gives a proof for the fact, well-established already by developmental researches of previous authors, that the phyllotaxis of the involucre is the direct continuation of that of the lower phyllomes.

§ 4. Discussion.

As stated above, the whorls of the appendages and the involucre are both heterotropically contort, but as the appendages are SW and the involucre LW, they may be called enantiotropic. The question to be discussed now is whether this fact may be explained on the same basis as the other cases of heterotropic aestivation. Our former cases were:

1. The heterotropic corolla (10, p. 40). The contort corolla whorl is alternating with an isomerous calyx, with eutopic origin of the sepals. The petal contortion becomes SW heterotropic by means of contact of the first petals with the sepals, after ternary and quinary parastichies.

2. The heterotropic calyx of the *Cistaceae* (10, p. 43). The contort whorl, consisting only of sep. 3—5, is preceded by two prophylls and by sep. 1 and 2, the latter pair alternating with sep. 3—5. The contortion becomes LW heterotropic by means of a contact with the preceding phyllomes after binary and ternary parastichies; a contact after quinary parastichies is impossible in this case for sep. 3 and 4.

3. The heterotropic androecium of *Sidalcea* (11). The contortion of the outer phalanges becomes SW heterotropic by means of a contact with the petals to which the phalanges are superposed.

To these three cases *Euphorbia fulgens* adds two others, and if possible their explanation should be based on the same principles.

A closer consideration directly shows that this is possible, if we start from the classical theory of the cyathium, as developed by Robert Brown, Roeper and Wydler, and set forth in detail by Eichler (1, p. 386). Thus we take the involucre to be a phyllome whorl, and the glands with the appendages to be commissural productions.

The involucral whorl on this basis is directly preceded by a varying number of spirally placed bracts, not forming a whorl. So it falls more or less in line with the calyx of *Cistus* with which it shares the LW heterotropy. The case is slightly different, as in *Cistus* only three sepals are contort, and they are preceded by two dimerous whorls, whereas the five involucral bracts of *E. fulgens* are preceded by 2—6 not whorled bracts.

Yet the only probable supposition is that the contact of involucral and lower bracts is according to binary and ternary parastichies, and if so, the contortion must needs become LW heterotropic.

As to the appendages, when these are structures intercalated between bracts and involucre, alternating with the involucral bracts, I already pointed out (10, p. 45) that their first formed member *a* will become skew in the SW direction by the contact with the involucral bracts 1 and 3. This appendage may determine its fellow members *b*—*e*.

Now that the involucre contortion is known, another possibility is that the skewness direction of all appendages is simply determined by contact with the superposed edges of the involucre, in the way demonstrated by fig. 2.

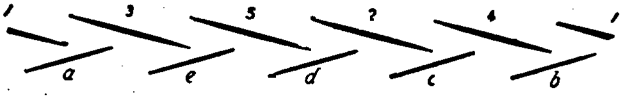

FIG. 2. Diagram intended to show how the appendages *a*—*e* by contact with the edges of the contort involucral bracts 1—5 may become enantiotropically contort.

In any case both forms of contortion in *E. fulgens* fit in very well with the general explanation of heterotropic contortion, and therefore give fresh support to this view.

Chapter II. Some remarks on the morphological interpretation of the cyathium in general.

The view that the cyathium is a condensed partial inflorescence is generally accepted in our day, the primitive view of a floral nature being definitely superseded.

It is only on details of the cyathium organization that different views are still held by recent authors. On two of these matters of dispute some remarks will be made here, namely on the nature of the involucre and the glands, and on the male partial inflorescences.

§ 5. The nature of the involucre and the glands.

According to the classic theory the involucre is formed by the concrescence of 5 (seldom 4—8) bracts, placed in a spiral phyllotaxis which is the continuation of that of the lower phyllomes. Between the involucral bracts commissural outgrowths are formed, the glands, sometimes provided with a dorsal petaloid appendage; this part of the theory is due to ROEPER, who first enounced it and gave good arguments for it (9, p. 33).

A wholly different view on the nature of the glands has been given by HABER, who takes every gland as representing a fused pair of modified secondary branches of a lateral inflorescence branch. Moreover GLÜCK and TROLL consider the commissural formations as the real phyllomes, and the involucral bracts (Zwischenzipfel) as interpetiolar stipules.

HABER's conception of the cauline nature of the glands (5, p. 700) is based on a study of the course of the vascular bundles in the involucre. On finding anew what had already been described for the greater part by WARMING long ago (14, p. 388) that the gland traces are double, and inserted laterally on the traces of the neighbouring involucral bracts, or sometimes on the traces of the male partial inflorescences which in their turn fuse below with the bract traces (see e.g. 5, p. 689, fig. 85—89), she writes about "primary axes" giving off "lateral axes" during their course through the cortex.

Such a view, based on a confusion between vascular bundles and stems, and on the belief that leaves and buds are originated by their outward growing traces, is to be discarded, the more as it clashes with all well established facts of external morphology.

It is on a basis of comparative morphology that GLÜCK develops his aberrant view according to which the glands and appendages are the real phyllomes, and the involucral bracts interpetiolar stipules (2, p. 321—326); Glück states namely that a resemblance between the cyathium parts and the inflorescence bract whorls points in that direction.

The same view on the same argument is adhered to by Troll (13, p. 169). Yet Troll realizes, what had been overlooked by Glück, that from the ontogeny and from the spatial relations between the cyathium parts some serious objections may be raised against such an assumption. He contends however (13, p. 299) that these difficulties may be overcome by supposing that the superposition of the bracts and the male inflorescences changes into an alternation of these two whorls.

In my opinion it is not difficult to show that the whole view of Glück and Troll is erroneous and that Roeper's theory is to be maintained, on the following arguments.

1. If the glands and appendages were the real phyllomes, one might expect to find traces in them of the phyllotactical spiral. Such traces have never been observed; see for instance Warming (15, p. 35, résumé p. 6, fig. 80).

2. The ontogeny clearly indicates that the involucral bracts arise before the glands and their appendages; according to Glück's view this should rather have been the reverse.

3. The appendages, if phyllomes, should not be SW but LW heterotropic, as they follow on phyllomes with a spiral phyllotaxis.

4. The involucral bracts, if commissural outgrowths, should not be formed in a 2/5 spiral, but one might expect them to arise either simultaneously or in a 1/5 order. That the actual order is that of the phyllotactical spiral, follows from the direct observation of the ontogeny (Warming 14, p. 387, 15, p. 20, rés. p. 4, Schmidt 12, p. 32, von Veh 13 a, p. 151), from the developmental order of the superposed male flower groups (same authors), from the flowering order of the subtended five main flowers (Wydler 17, p. 453, 19, p. 24; own observation in *E. fulgens,* where it was very evident that the main flower in front of the first involucral bract flowers first, followed by the main flowers in front of bract 2—5 in a regular order, the second flowers of the cincinni coming afterwards), and from the aestivation of the involucre in *E. fulgens.*

5. The involucre, if commissural, should not be LW but SW heterotropic, as the skewness direction of the bracts should be

determined by the underlying appendages.

6. The male partial inflorescences instead of being superposed to the involucral bracts should alternate with them; a change, whether ontogenetical or phylogenetical, of this superposition into alternation, as TROLL suggests, would be unparalleled in the branching of Dicotyledons.

Against all these serious objections GLÜCK and TROLL can only bring forward a certain likeness in plastics, a feature the small importance of which in morphological questions has always been recognized.

So there is no doubt that only the classic view in this respect is correct.

§ 6. The male partial inflorescences.

In 1843 WYDLER wrote: "Die fünf monandrischen, die weibliche Centralblüthe umgebenden Blüthenreihen von *Euphorbia* sind als eben so viele Wickel zu betrachten, wie aus der Stellung der Bracteen (Vorblätter) der einzelnen monandrischen Blüthen, als aus der Aufblühfolge jeder Reihe hervorgeht" (16, p. 409).

This view has since been accepted by nearly all morphologists and has been incorporated into the classic theory, as an essential part of it. It has however been doubted in the twentieth century by SCHMIDT and by HABER.

SCHMIDT, studying the ontogeny of the cyathia in a number of *E.* spp. found in all of them (12, p. 35) that in the male partial inflorescences the third flower is not developed by branching of the second, but is derived from the first flower; in the same way the second flower produces the fourth, the third the fifth etc. From these observations he drew the conclusion that the male inflorescence is not a cincinnus, but a dichasium, producing two monochasia after its first ramification.

This result was corroborated by a study of the vascular bundle course, the traces of the right and those of the left flower row forming two separate sympodial strands (12, p. 14, fig. II).

The same view has been defended by HABER (5, p. 693) on the basis of the latter argument of the vascular bundle course only.

In my opinion both arguments are of little value. In a real cincinnus of flowers any flower no doubt is a branch of the next older flower of the other row. By the formation of a spurious axis this relation may be obscured during or before the visible developmental stages, so as to give the appearance of two rows of lateral branches on a continuous main axis; we may recall in this connection GOEBEL's attempts to homologize the cincinnus of the *Boraginaceae* with a dorsiventral raceme (3, p. 406—422).

In the case of a condensed cincinnus with a contracted spurious axis, like the male partial inflorescence of the cyathium must be according to the classic theory, the two rows of seemingly lateral flowers may quite well show a coherence of the row members during their ontogeny.

Moreover the fact of such a coherence described by SCHMIDT has been denied by MICHAELIS (8, p. 92) who did not succeed in finding any trace of it in *E. salicifolia, E. geniculata* or *E. splendens* (ibid. pl. 40, fig. 11, 13) or in *Pedilanthus.*

As to the formation of a right and a left sympodium of floral traces, this may be quite well explained by the same condensation; we might even say that another condition might hardly be expected.

Of course, by the fact that the arguments given by SCHMIDT and HABER are not conclusive, the presence of dichasia ending in cincinni in cyathia of some species is not yet excluded, and in the case of *Anthostemma Aubryanum* the involucral bracts without any doubt subtend dichasia or even trichasia with at least three dichasial ramifications and few monochasial endings, as is shown by the diagram given by MICHAELIS (8, p. 40, fig. 1).

In the cyathium of the genus *Euphorbia* the common condition however is that of simple cincinni of male flowers, without a dichasial beginning. This statement, which of course may appear to be subject to exceptions when a greater part of the innumerable species of the vast genus is examined, is based on the following arguments.

1. When the male flowers are found to be arranged in two straight rows, emanating from the anterior side of the primary flower, as is the case in nearly all species, the assumption by SCHMIDT of a double cincinnus or a double screw is untenable. A double cincinnus would require the presence of four flower rows, a double screw that of two twisting rows; the only possible form of a double monochasium would be that of a double sickle, a form of inflorescence quite alien to the *Euphorbiaceae.*

2. If the double row were a double monochasium, the change from the initial dichasium into the later monochasial mode of branching should be subject to some variation in place, so that the number of dichasial branchings occasionally might be either two or more, or nought.

3. In a double monochasium the two monochasia are independent. A regular spatial alternation of the flowers of the two rows, as observed in most E. spp., might still be due to packing, but the regularly alternating order of flowering and especially the equal development of the two monochasia, never one row having two or more members short as compared with its neighbour, would be against all expectation.

Especially when we think of the strong tendency in *Euphorbia* inflorescences towards furthering of the highest laterals, does this argument become very strong.

For a thorough discrimination of the conditions in the male flower groups, the best criterion might have been derived from the distribution of the bracts subtending the separate flowers. As these bracts usually are ill-developed or have assumed pappus-like shapes, most species are not suitable investigation material in this respect. But it would not be surprising if some not yet investigated species should yield better cases and in literature there are already some indications of such conditions.

In the first place we have the short statement by no less an authority than WYDLER, quoted above and repeated twice in a somewhat more detailed form later on (18, p. 433, 19, p. 24), and further a more detailed statement by HIERONYMUS for several species (6, col. 174), that two rows of bracts are present between two partial inflorescences, each row having one bract near every flower, the primary flower excepted.

The last case to be mentioned is that of *E. Tessmannii*, described by MANSFELD, where every partial inflorescence only contains two flowers, placed symmetrically to the left and the right, and each subtended by a narrow bract. Mansfeld supposes that here the primary flower has aborted and that the two flowers represent the products of the first dichasial branching. Though this supposition is quite possible, it is not to be considered as established without further substantial evidence.

Summarizing we come to the conclusion that the classic theory about the male flower group as well as that about the construction of the involucre stands the test against all modern attacks; this is only a new example of the great internal strength of the old morphology, a strength which is underrated by many modern botanists.

Of course the classic theory has its deficiencies and it may still be corrected and completed in details. But in the main part it is no doubt correct.

Summary.

A. Euphorbia fulgens.

1. The aestivation of the cyathium appendages is SW (= short way) heterotropically contort. When in some cyathia the aestivation is less regular, and an individual appendage is wholly overlapping, this is usually appendix *a*, between the involucral bracts 1 and 3, sometimes *b*, between the bracts 1 and 4.

2. The aestivation of the involucral bracts usually is LW heterotropic. In a minority of cases the aestivation is different; the departures from contortion are nearly always returns to eutopy, even so much that in a considerable minority of cases a complete eutopic aestivation is reached.

3. The facts reported sub 1 and 2 give a fresh support to the views expressed earlier about the determination of the contortion direction in heterotropic aestivation. At the same time they give new evidence for the classic theory of the cyathium.

B. The cyathium in general.

4. The view of HABER that the glands represent cauline structures is to be discarded.

5. The view of GLÜCK and TROLL that the glands are phyllomes of which the appendages represent the laminas and the involucral bracts the stipules, is not to be accepted.

6. The view of SCHMIDT and HABER that the male partial inflorescences in the cyathium of *Euphorbia* are dichasia with monochasial endings, is not supported by any facts.

7. The classic theory of the cyathium, as expounded by EICHLER, is to be maintained.

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Groningen, Febr. 1937. the Government University.

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