The Development of the Flower of the Dipsacaceae.¹

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With Plates VII and VIII and five Figures in the Text.

THE development of the flower of the Dipsacaceae, according to the publications of Buchenau (1), Payer (6), van Tieghem (8), and my own former investigations (7), seems to be clear. There are, however, several questions not yet solved. Some more exact microtechnical work and the precise observation of the development are required to answer them.

These unsolved questions are as follows: 1. How does the carpel appear during the successive development of the different parts of the flower, and how is it a participant in the formation of the ovary? 2. Is the wall of the ovary an axile or a carpellary formation? 3. What is the arrangement of the vascular tissues of the flower-parts?

I wish to answer these questions, discussing the successive development of the flower-parts and the arrangement of their vascular bundles after having given a general description of the flower?

I. THE FLOWER.

According to van Tieghem's precise definition, *the flower of the Dipsacaceae* is nothing but a single-flowered capitulum, which appears in the axil of a bract closely surrounded with an involucl. The stalk of this partial capitulum usually fails to develop appreciably; it elongates only in cases of proliferation. The involucl originates in four joined bracts, as is a general rule in the family of the Dipsacaceae. These four bracts, in prolific examples, may also form separate diverging involucls; even the number of the bracts may increase, as has been observed in several irregular cases. The situation of the four leaves of a normal involucl is median transverse, and it surrounds the inferior ovary, resembling a closed tube. After fertilization it grows longer, enclosing the genuine fruit, and as it is a closed integument, it falls off together with the fruit. The flower itself is hermaphrodite; its single leaf-zones are situated at the top of the inferior

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ovary, forming three whorls (calyx, corolla, stamens). The zone of the sympetalous corolla in the genera *Knautia*, *Dipsacus*, *Succisa*, *Succisella*, and *Cephalaria* is four-membered. The four episepalous diagonal stamens with their filaments grow on the top of the corolla. The calyx is situated on the spindle-shaped ovary and has a various number of members: in the tetramerous genera ordinarily four, in the pentamerous genera five. The inferior cupular ovary has only one cavity with a single anatropous pendent ovule. The situation of the latter is epitropous introrse. The stigma is double in the groups *Knautiae* and *Scabiosae* (van Tieghem's 'Knautiées et Scabiosées'), but it is simple in *Dipsacus* and *Cephalaria*.

To complete my former investigations of the flower of the *Knautiae*, which have two stigmas and no bract, I chose the flower of *Cephalaria* as the subject of my present study. This flower is completely tetramerous, with a single stigma and bract. The flower with a single stigma shows the greatest reduction, and the presence of a bract is necessary for any conclusions possible as to orientation.

II. THE DEVELOPMENT OF THE FLOWER.

All authors, since Payer's investigations (6), agree that *the succession of the development of the different flower-parts* is uniform throughout the family. The four protuberances of the involucl appear first. According to Gjurašin (4) the two median protuberances appear first, and the two transverse ones later (Pl. VII, Figs. 1, 2). The flower-protuberance is still closely covered by the bract. Alternately with the four protuberances of the involucl arise the four protuberances of the calyx (Pl. VII, Fig. 3), and these are alternate with those of the corolla, which develop still later. During further growth, the development of the zone of the gamosepalous calyx (*k*) is slower than that of the gamopetalous corolla and of the involucl. The development of the corolla (Pl. VII, Fig. 5) is the most rapid. Alternating with the median-transverse protuberances of the latter, the protuberances of the stamens appear. The common basal part of the staminal and corolla whorls elongates to become the tube of the corolla (see Textfig. 2), therefore the stamens and the tube of the corolla have grown together at their lower part. On Pl. VII, Fig. 6, there is shown the stage in which the four median-transverse protuberances of the involucl have become strong, and, what is more, there appears between them a protuberance diagonally situated. The teeth of the calyx situated diagonally are the strongest. Among the four protuberances of the corolla, the one in the front is a little larger; its situation is median, near the bract (*b*). The figures of Pl. VII show nearly the same gradations as Payer's Figs. 1, 2 (relating to *Dipsacus*). It is a pity, however, that in Payer's figures no

orientation is shown, and the parts of the calyx are not shown except in the more developed state.

During the further development there are to be seen other and more important differences, when the ovary is in the course of formation. According to Payer the development of the ovary of *Dipsacus* (with one stigma) takes place so that at the edge of the carpel cavity there appear not two antero-posterior protuberances, but a single one (l. c., p. 630), which elongates and becomes the style. The situation of this horseshoe-shaped protuberance is transverse on the right in Payer's drawing (l. c., Pl. 131, Figs. 12, 13). The ovule begins to develop from the transverse (left) side (l. c., Pl. 131, Figs. 15, 16). Van Tieghem comments on this observation and drawing of Payer's, supposing that Payer sees the origin both of the ovary and of the style in the same anterior carpellary protuberance, while the posterior carpel is assumed to be totally missing. Eichler's and van Tieghem's statements are not based upon actual observation of the development, but are deductions from the adult condition. It has been already stated by Buchenau (1) that the pistil originates with the median-dorsal (posterior) carpel. According to Eichler the median-posterior ovule appears on the suture of the carpel, and therefore this carpel must have a median-anterior situation. The papillose, furrowed part of the stigma looks forward. This situation may be explained by the posterior carpel; van Tieghem assented to this opinion too, concluding that the carpel of the *Scabiosae* with two stigmas originates in two protuberances, but that only one of them takes part in the formation of the ovary. On the other hand, from the median-anterior protuberance of the *Dipsacaceae* and *Cephalariae* with one stigma, the ovary only develops; the style and the stigma originate from the posterior protuberance.

The results of my own investigations do not support these views; I find that on the one-stigated *Cephalariae* there appears only one carpel-protuberance, the situation of which is median-posterior, or it is protruded in the direction of the diagonal. *From this protuberance develop the style and the ovule, but the ovary is a cupular (axial) formation.* This protuberance is a rudiment of four carpels, as I shall show later on when discussing the formation of the tissues. This result may be proved by the following phenomena: In the early stage of the development of the flower-bud the conditions are just the same as in the genera with two stigmas. The top of the flower-protuberance is concave. This cavity is already visible when the protuberances of the involucl and those of the calyx and corolla appear. (See Text-fig. 1.) This cavity becomes more and more deep, just as in the case of the *Knautiae*. In Text-fig. 2, which is a nearly median, longitudinal section of the stage shown in Pl. VII, Fig. 6, there is a protuberance to be seen (*g*) which is the carpel protuberance. This, together with the basal part of the opposite median-anterior petal outgrowth (*c*), borders a depres-

sion which may be called the *ovary-groove*. The situation of the protuberance may be seen also in Pl. VII, Figs. 7, 8 (g). This protuberance is horse-shoe-shaped. The flexure of the 'horseshoe' is lying on a higher level; its situation is median posterior or diagonal; its two extremities become gradually lower and they border a slit which opens into the ovary-groove. The shape of the ovary-groove may be seen in Pl. VII, Fig. 8. This state of development is in accordance with Payer's (6) drawings on Pl. 131, Figs. 13-16. The horseshoe-shaped protuberance, however, is shown as trans

TEXT-FIG. 1. Median longitudinal section of the flower-protuberance of *Cephalaria elata* (from a microphotograph). *br*, bract; *c* and *c'*, the median-posterior and the median-anterior petal outgrowth; *i*, involucre outgrowth; *k*, calyx outgrowth. $\times 80$.

TEXT-FIG. 2. Median longitudinal section of the flower-protuberance of *Cephalaria elata* in a more developed stage. *a*, stamen attached to the basal part of the corolla; *b*, bract; *c* and *c'*, the median-posterior and the median-anterior lobe of the corolla; *g*, the beginning of the development of the carpel outgrowth; *i*, involucre; *k*, calyx; *stete*, the formation of the procambial tissue in the stalk. $\times 16$.

verse and the depth of the ovary-groove has been wrongly figured. At this stage its depth is never greater than that shown in Pl. VII, Fig. 8, i.e. the bottom of the ovary-groove is at the most at the level of the union of the calyx and corolla; it only becomes deeper later.

The growth of the horseshoe-shaped protuberance of the carpel and the formation of the ovary-groove may be traced gradually in Pl. VII, Figs. 9-13. The development of the style is figured in Pl. VII, Figs. 14-19,

and Pl. VIII, Fig. 20. The rapid growth of the horseshoe-shaped protuberance begins at its median-posterior part at the flexure, so that the 'horseshoe', which is at first low-lying, rises more and more and the slit becomes oblong (Pl. VII, Figs. 17, 18). After this follows the growth of the basis of the horseshoe, in consequence of which the horseshoe becomes a ring. From this ring develops the papillose part of the stigma; the styler part originates in the basal part of the ring. The stigma extends itself and, as may be seen in Pl. VIII, Fig. 20, it acts a part as receiver of the pollen (*p*). It is simple, not bifurcated as in the Knautiae.

Together with the development of the style and its stigma described above, the bud also grows in the longitudinal direction and thickens. Changes set in also in the ovary-groove. It is thin, resembling a slit (Pl. VII, Fig. 11). The style (*s*) with the stigma (*st*) is situated at the top, and in its broader part below there appears a protuberance (*o*). This protuberance grows rapidly to form the ovule (Pl. VII, Fig. 13). The part below the junction of the ovule (shaded in Pl. VII, Figs. 9–13) grows just as described by Goebel (5) for *Valeriana*, and by me for the Knautiae (7). This part is the part of the axis between the protuberances of the involucrel (*i*) and the protuberances of the calyx (*k*), i.e. the receptacle of the flower which finally surrounds the ovary-groove completely. The introrse ovule is hanging in the ovary with an anterior suture and a micropyle looping backwards and upwards (Baillon, 'Hist. des plantes', vii, 1880, p. 520), just the opposite to that described by Payer for *Dipsacus* (see van Tieghem (8), p. 185. This situation, however, is not uniform, and it varies in accordance with the position of the flower in the inflorescence. The longitudinal symmetry-plane of the ovule may decline from the median to the transverse direction in a different degree.

During the further development of the flower (Pl. VIII, Figs. 21–9) on the development of the cupular ovary follows the development of the involucrel (*i*). The growth of the calyx (*k*) is limited. As a general rule in the flowers of Dipsacaceae the median-anterior petal-lobe covers the two transversally situated lobes and the posterior petal-lobe is covered by the transverse lobes. At the time of blossoming, in accordance with the proterandry, the stamens are ripe earlier than the pistil, their bent filaments become straight, and in the succession the two posterior stamens rise earlier than the two anterior ones (Pl. VIII, Figs. 25–7). The difference in the behaviour of the two anterior stamens is already to be observed at an early period of the development; it is probable that the phenomenon is a compensatory one, as the cause of it may be the powerful growth of the median-anterior petal-lobe which is in connexion with this pair of stamens. On the other hand, the retardation of the growth of the median-posterior petal-lobe assists the quick development of the two posterior stamens, with which it is in connexion. A considerable elongation of the style takes place after pollination

when the development of the cupular ovary of the ovule and of the involucl has been completed (Pl. VIII, Fig. 29).

During the development of the flower the bract plays an important part as a protector, thoroughly covering and surrounding the little bud in its boat-shaped cavity (Pl. VIII, Fig. 23). While the bud is growing, the basal part of the bract grows too; its end bends over the top of the bud (Pl. VIII, Fig. 24). The outer side of the petal-lobe, covering the bud and also the outer side of the bract, is generally thickly hairy; or, if the latter is bare, then it has a red colour caused by anthocyan. During the blossoming the tip of the bract is bent back, but the lower part still surrounds the involucl.

III. THE ARRANGEMENT OF THE VASCULAR BUNDLES.

Only the arrangement of the vascular bundles in the development of the flower, which are of importance in connexion with the morphological value of the ovary, will be considered. The joining of the vascular bundles has been determined by means of a series of longitudinal and cross-sections made with the microtome. The relations observed in this way have been compared with the situation of the vascular bundles in a typical tetramerous flower.

For comparison I have figured the joining of the vascular bundles of a pentacyclic tetramerous flower with a superior ovary (Text-fig. 3). In Text-fig. 3, 1 the four leaves of the involucl, the four leaves of the calyx, the four petals, the four stamens, and the four carpels, situated alternately, are seen. The primary median vascular bundle of each has been indicated with a white circle. It is seen that the vascular bundles of the involucl, those of the petals, and those of the carpel are situated in the median-transverse line. The position of the vascular bundles of the calyx and of the stamens is diagonal. In the later drawings the flower-leaf whorls are seen to have been gradually inserted in the axis. In the axis first appear the four median-transverse carpel bundles (g); the four bundles of the stamens (a) will soon be inserted between them diagonally (3). There are now eight vascular bundles in the cross-section of the axis and they have their woody portions directed inwards forming a 'eustele'. To the eight bundles of this eustele join the vascular bundles of the petals in the median-transverse line ($g+c$), those of the calyx in the diagonal line ($a+k$), finally the bundles of the involucl in the median-transverse line ($g+c+i$). The result is that in the axis there are also eight procambial bundles forming a eustele. Later on, however, these eight bundles join to form a ring. This might be the course of formation of the procambial joining of the vascular bundles of a tetramerous flower theoretically, based upon the observations made on the Dipsacaceae.

In the flower of the Dipsacaceae, however, the manner of union of the

TEXT-FIG. 3. Theoretical ground-plan of the junction of the vascular bundles of a tetracyclic tetramerous epigynous flower. *i*, the whorl of the involucre; *k*, the whorl of the calyx; *c*, the whorl of the corolla; *a*, the whorl of stamens; *g*, the whorl of the ovary. The white and black discs indicate the situation of the vascular bundles.

TEXT-FIG. 4. Ground-plan of the flower and the junction of the vascular bundles in the genus *Cephalaria*. 1-6 are ground-plans of the levels indicated in Text-fig. 5 by horizontal double lines and by corresponding roman letters; lettering as in Text-fig. 3.

vascular bundles has been altered by the fact that the situation of the ovary is inferior owing to the reduction of the carpel zone. Text-fig. 4 shows the arrangement of bundles in the *Cephalariae*, in the same way as in Text-

fig. 3. The single figures of drawing 4 show different levels, the situation of which is indicated by numbered lines in Text-fig. 5.

Text-fig. 4, 1, shows the ground-plan of the flower at the level of the stigma where the stamens branch off. The involucl is shown as lengthened as far as this level. The involucl is gamophyllous with four median-transverse lobes; this is followed by the united calyx and alternately by the corolla, and the middle bundle has also been figured in each of them. Now it is obvious that the carpel zone, following on the four diagonally situated stamens (indicated by the four circles), apparently consists of a single carpel only, but it has three vascular bundles, one of them median-posterior and two transverse, the median-anterior being missing.

TEXT-FIG. 5. A sketch of the longitudinal section of the flower of *Cephalaria*, showing the union of the vascular bundles. The double lines I–VI indicate the different levels at which the diagrams of Text-fig. 4 were taken. The right half of the drawing represents the median-posterior plane, the left half shows the diagonal plane; *a*, the vascular bundles of the stamens; *c*, those of the corolla; *g*, those of the ovary; *i*, those of the involucl; *k*, those of the calyx; *σ*, those of the ovule, which have been indicated by interrupted lines.

Text-fig. 4, 2, shows the insertion of the calyx on the top of the inferior ovary. At this level there are to be seen all eight vascular bundles of the 'eustele': the four median-transverse petal-bundles (*c*) and the four diagonal bundles of the stamens and calyx (*a + k*). Three bundles which originate in the style do not join the bundles *g*, but three of the *g*-bundles form a separate eustele which has been thrust away from the centre in a backwards or diagonal direction. This change of position is intelligible when we consider that the middle of the axis has been occupied by the cavity which opens into the inner part of the ovary, which is relatively important at the beginning of development (Pl. VII, Figs. 10–13). At a little lower level the funicular bundle *σ* of the pendent ovule enters, just at the point

where the missing fourth bundle, *g*, would be situated (Text-fig. 4, 3 and 4).

The distribution of the vascular bundles shown in Text-fig. 4, 4, above, is characteristic for the whole ovary. Throughout the whole length of the wall of the ovary, all the eight vascular bundles are to be found situated in the median-transverse and diagonal planes, there being bundles of the whorls of the calyx, corolla, and stamens. Further, in the posterior-median or diagonal region the 'ninth vascular bundle',

as this stele (*g*) has been called by van Tieghem (8), is to be seen. Van Tieghem did not know the structure and origin of this bundle; he has only distinguished it as a bundle much larger than the others and running into the ovule. I described it in like manner in dealing with the Knautiae (7), and Fodor (3) has done the same in his work on the Cephalariae. The structure of this vascular bundle, however, shows its hadrocentric nature; it is not a collateral bundle as are all the eight others; while tracing its development it is possible to determine that it originates in four collateral bundles with their woody portions turned inwards; they actually form the central stele of the axis. The eight peripheric bundles join this stele (Text-fig. 4, 5) at the bottom of the ovary. The monocyclic eustele (Text-fig. 4, 6) is seen restored in the stalk and shows an arrangement identical with that figured in Text-fig. 3, 6. The final result is a collateral ectophloic siphonostele. If the *g*-bundles would go in the wall of the ovary, surrounding its cavity in median-transverse direction, before the *c*-bundles, then one might suppose that the tissue which lines the inside of the ovary has a carpellary origin. But it is not so; the carpels do not take part in the building of the wall of the ovary. On the other hand, the independence of the *g*-stele, even the fact that it often parts from the wall of the ovary, shows directly that this stele must be a rudiment of the separating wall of the ovary, which is a general formation in the series of the Rubiales. Its connexion with the wall of the single cavity of the ovary may be explained by the fact that other cavities do not develop at all. It might be concluded from this circumstance that the *g*-stele is a direct lengthening of the top of the axis.

IV. SUMMARY.

From the investigation of the development of the floral leaves it may be concluded that the wall of the ovary as a whole is an axile structure, originating in that part of the axis which corresponds with the internode between the insertions of the calyx and corolla. In the wall of the ovary as in an axis there are the eight vascular bundles of the flower whorls, the bundles of the gynoecium still forming for a while a separate stele. From the construction and development of this separate stele one may conclude that it is a rudiment of the ancestral diaphragm (partition wall) or centric column, and it actually shows its ancestral tetramerous structure. Of the four original carpels the median-anterior alone forms the ovule; the other three (the one median-posterior and the two diagonal) form the simple style. The change in the situation of the stele, which is pushed backwards in the median plane, makes it appear that there is only one median-posterior carpel which gave origin to both the style and the ovule.

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EXPLANATION OF FIGURES IN PLATES VII AND VIII.

Illustrating Professor Szabó's paper on the Development of the Flower of the Dipsacaceae.

PLATE VII.

Figs. 1-8. The early stages of development of the flower of *Cephalaria elata*. *a*, stamens; *b*, bract; *c*, corolla; *g*, the protuberance of the carpel; *i*, involucl; *k*, calyx.

Figs. 9-13. Further stages of development of the flower. *a*, anthers; *b*, bract; *c*, corolla; *c'*, median-anterior lobe of the corolla; *i*, involucl; *k*, calyx; *o*, ovule; *s*, stigma; *st*, style.

Figs. 14-19. The development of the stigma and style. 1-3, the horseshoe-shaped protuberance of the carpel; *a*, stamens; *c*, corolla; *i*, involucl; *k*, calyx; *p*, pollen.

PLATE VIII.

Fig. 20. The fully developed stigma.

Figs. 21-29. The development of the bud and flower of *Cephalaria elata*. 21. Left side view. 22. Median-posterior view. 23-4. Side view with the bract. 25. Emergence of the two stamens. 26. Emergence of two other stamens; the involucl has been removed. 27. The male (staminal) stage without the ovary. 28. At the time of elongation of the style; half of the corolla has been removed. 29. The later (female) stage. *i*, involucl; *k*, calyx; *o*, ovary; *p*, bract.

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