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13 Studies in Flower Structure IV. On the Zygnaceae of Papua & Related genera. Ann Bot N.S. Vol II, 1938 pp 649-664

14 Studies in Flower structure V. On the Interpretation of the Petal. Corona in Hydrocharis. Ann. Bot N S Vol III 1939 pp 337-346

15 Studies in Flower Structure VI. ~~Same~~ On the Reputed Vascular Supply to the Apices of Reproductive Shoots, with special reference to Selaginella Ann Bot N S Vol IV, 1940, pp 617-628

16 Studies in Flower Structure VII. On the Zygnaceae of Peru, with considerations of Parazygn. Ann Bot N S Vol VI 1942 pp 43-68

Contents

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These papers grew out of the following idea, which I copy from a letter I wrote to E. A. Newell Arber on January 29, 1908:—
"A point I feel very keen on is that there is a comparatively untouched field in the application of microtome methods to the smaller problems of anatomy. The general tendency is to look on the microtome as suitable only for cytological work, but my apprenticeship in seedling work made me realise how valuable the power of the microtome is in following out the course of vascular structures. The very [illegible] accuracy it gives you is something infinitely beyond hand sections. It was brought home to me when I worked out some seedlings of the *Scitamineae* & only got it out after days of observation on the serial sections of one single seedling, following the highly complicated structure almost (in some cases quite) tracheide by tracheide from section to section. The exact orientation of successive sections in the series one cannot get by hand.... I believe that all sorts of little points, & even some big points, may come out if one turns the microtome on to flower anatomy."

Agnes Arber

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wf I

A. ARBER

STRUCTURE OF THE ANDROECIUM IN PARNASSIA

[Annals of Botany, Vol. XXVII, No. CVII, July, 1913]

The present writer holds that the relationship with the Hypericineae is closer than was supposed by Drude, and considers that the affinity between *Parnassia* and the Saxifragaceae has, in recent years, been somewhat over-estimated.

Balfour Laboratory,
Cambridge.
December 22, 1912.

EXPLANATION OF PLATE XXXVI.

Illustrating Mrs. Arber's paper on *Parnassia*.

All the figures represent sections through the vascular tissue of the stamen of *Parnassia palustris* magnified 450 diameters. The sections are so placed that the centre of the flower would lie to the right of the diagram in each case. *xy.* = xylem; *pr.* = protoxylem; *cpx.* = centripetal xylem; *cfx.* = centrifugal xylem; *ph.* = phloem.

Fig. 1. Transverse section of filament showing ring-like xylem, with protoxylem attached to the inner face of the ring on the dorsal side. The numerous small groups of phloem are arranged round the xylem and at some little distance from it.

Fig. 2. Radial longitudinal section through a bundle such as that shown in Fig. 1.

Figs. 3, 4, and 5. Transverse sections at different levels of the filament and connective of the same stamen.

Fig. 3. Section to show discontinuous xylem ring. Xylem only represented.

Fig. 4. Section at a higher level to show centripetal xylem entirely detached from centrifugal xylem.

Fig. 5. Section through the connective to show the xylem complex.

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ARBER, AGNES

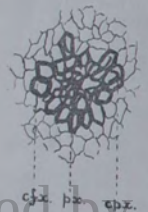
THE ANATOMY OF THE STAMENS IN CERTAIN INDIAN SPECIES OF PARNASSIA

[Annals of Botany, Vol. XXIX, No. CXIII, January, 1915.]

position. In herbarium material, the phloem cannot be recognized with certainty. As regards the xylem, the bundle closely recalls certain forms assumed by the vascular structures in the filament of *P. palustris*, as may be seen by comparing the figure of the present note with Pl. XXXVI, Fig. 1 of my previous paper. (In both these figures the adaxial side of the stamen lies to the right of the diagram.)

In the next species, *P. Wightiana*, the bundle is small, and, though the xylem opens out in the connective, no other sign of complexity can be detected, except that there are occasional indications of a centrally-placed protoxylem in the filament. This Indian species has thus reached a stage of reduction in the stamen-anatomy comparable with that obtaining in the American form *P. montanensis*.

In *Parnassia ovata* and the minute species *P. pusilla*, the bundle is very small. I have found no trace here of the anatomical complexity in the filament, which seems to be confined to the larger members of the genus with stouter stamens. These two species may thus be compared with the American form *P. parviflora*, whose slender filaments are traversed by a simple bundle. It may be recalled that Hooker and Thomson[1] have suggested that *P. pusilla* and *P. ovata* may perhaps prove to be merely forms of *P. nubicola*. If this were so, it would confirm the view that their stamen-anatomy represents a stage in reduction from the more complex type found in *P. palustris*, *P. fimbriata*, and *P. nubicola*.



Parnassia nubicola, Wall. Transverse section of xylem group in filament a short distance below insertion of anther. The adaxial surface of the stamen would lie to the right of the diagram. *cfx.* = centrifugal xylem; *px.* = protoxylem; *cpx.* = centripetal xylem. (× 656.)

Since the presence of additional xylem elements on the adaxial side of the filament bundle has now been recorded in three species belonging to two different Sections of the genus *Parnassia*, and natives respectively, of Europe, America, and Asia, and since in the only cases so far examined in which this complexity is absent, the bundle may reasonably be regarded as having undergone reduction, we may infer that the structure in question was probably characteristic of the common progenitor of the genus. As I have previously suggested, the unique features observed in the anatomy of the androecium may be interpreted as indicating that the single stamen of *Parnassia* has been derived by reduction from an ancestral stamen-fascicle.

AGNES ARBER.

Balfour Laboratory, Cambridge,
June 5, 1914.

[1] Hooker, J. D., and Thomson, T.: Praecursores ad Floram Indicam. Journ. of Proc. Linn. Soc. Bot., vol. ii, 1858, p. 78.

Copy marked for slide numbers . 3

STUDIES IN FLORAL MORPHOLOGY

I. ON SOME STRUCTURAL FEATURES OF THE CRUCIFEROUS FLOWER 3

BY

AGNES ARBER, M.A., D.Sc.

From the New Phytologist, Vol. XXX, No. 1, 1931

CAMBRIDGE
AT THE UNIVERSITY PRESS

PRINTED IN GREAT BRITAIN

again to the floral anatomy of the Dicotyledons, with a renewed hope of obtaining, from a more modern standpoint, some clue to the understanding of the androecium. But in deciding to return to the subject I have also been influenced by reading the literature dealing with the interpretation of the gynaeceum. The study of the controversy in which this subject has become involved, has convinced me that our comparative knowledge of floral structure and anatomy is altogether inadequate to bear the weight of theory which has been built upon it. This unsatisfactory state of things is largely due to the fact that much of the work dates from pre-microtome days. The result of the attempt to study floral structure by means of hand-sections alone is often an artificial simplification of the actual facts, since many of the finer details of bundle behaviour are inevitably lost; unlignified strands, especially, are liable to be ignored. Moreover, in a series of hand-sections the orientation is not determined automatically, which is both a grave defect in itself, and also makes it impossible to follow the bundles from section to section with any confidence, especially in cases in which accuracy can only be secured if these bundles are pursued element by element. Again, hand-sections throw no light upon the spatial relations of the parts, except at levels at which they are connected. For these reasons, hand-section work in floral anatomy can only have a limited value, and although there are in existence certain excellent individual studies of flower structure based upon microtome sections, they cover at present a relatively narrow field. We still stand in need of a descriptive treatment of the subject on broad comparative lines before there can be any justification for an interpretation of the flower based on structural evidence. In this, and I hope in later papers, I am attempting some small contribution towards the first step—an understanding of the actual facts of flower structure—normal and teratological. The present instalment deals with the organisation of the normal flower in certain Cruciferae. The structure in the species examined is first described (pp. 12–25) and a number of points arising out of these descriptions are then discussed (pp. 25–39)[1].

2. DESCRIPTION

Throughout the descriptions I use the expressions "valve strand" and "replum strand" in a purely topographical sense, to distinguish

[1] An abstract of part of the present paper was given in the Discussion on Floral Organisation, Fifth Intern. Bot. Congress, Cambridge, Aug. 20, 1930.

bundles occupying a certain relative position in the gynaeceum; these terms have the advantage of involving no theory as to the carpel-constitution of the gynaeceum.

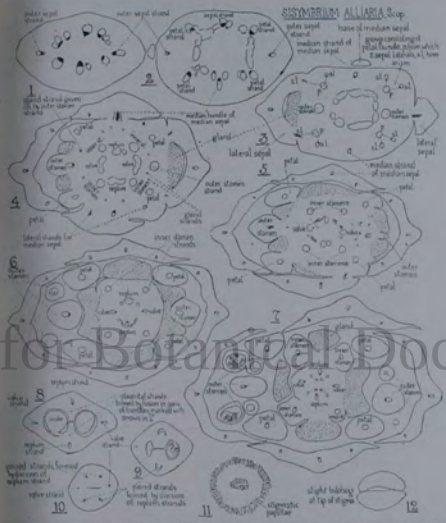


Fig. 1. *Sisymbrium Alliaria*, Scop. *1–12*, transverse sections from a slightly oblique series from below upwards through a flower (× 34 *circa*); glands dotted. In *3*, *p.*, petal bundle; *sl.*, sepal laterals given off from petal bundles. In *12*, the papillae, being vertical at the top of the stigma, do not show as outstanding objects in transverse section. For description of this series, see text, pp. 13, 14.

(i) *Sisymbrium Alliaria*, Scop.

Figs. *1*, *1–12*, above, represent transverse sections from a series passing through a flower of Garlic Mustard from the pedicel just below the flower (Fig. 1, *1*) to the stigmas (Fig. 1, *12*). This series of

sections is not quite transverse, so that on the right hand a slightly lower region of the flower is cut than on the left. In Fig. 1, *1*, the ellipse of bundles is broken by the outward passage of the median strands for the lateral pair of sepals, which are the first-formed members of the flower. In Fig. 1, *2*, these bundles are approaching the periphery of the receptacle, and the four bundles for the petals are passing out of the ring in the diagonal planes. The median strands for the pair of front and back sepals are also leaving the ring. To right and left the gap left by the outer sepal bundles is being bridged. In Fig. 1, *3*, the lateral sepals are coming into view; to the left the base of one of the glands characteristic of the Crucifers is visible within the sepal. Each petal bundle, *p.*, has given off two bundles, *s.l.*; the bundle triads thus produced are connected in the diagram by dotted lines. Of the two branches given off by each petal bundle, one enters the margin of the adjacent outer, and one, the margin of the adjacent inner sepal; they form lateral veins for these members. A bundle for each of the two outer stamens has passed out in the lateral plane in which the median bundles for the lateral sepals moved out at a slightly lower level. In Fig. 1, *4*, four bundles for the inner stamens are passing out in the diagonal planes, following the directions previously taken by the petal bundles. The glands are supplied by strands which are so delicate that I have only been able to trace the origin of one, which I found to arise from an outer stamen bundle.

The departure of the four inner stamen bundles leaves four gaps in the cylinder, separating four vascular groups lying in the planes of the valves and replums (Fig. 1, *4*). Horizontal branches from these masses pass across the gaps (*5*, *6*), and from these transverse bridges, four minor vertical strands arise, which thus have a mixed origin from vascular tissue in the planes of the valves and replum. These vertical strands move inwards (*7*) and fuse in pairs within the replum strands, forming placental bundles (*8*). At a level towards the top of the loculi (*9*), the replum strands divide into two. This division is complete in *10*. The papillose stigma (*11*) is slightly bilobed at the tip (*12*); the lobes, as usual in the Crucifers, stand above the replums.

(ii) *Sisymbrium orientale*, L.

Sections through the very young inflorescence axis of *Sisymbrium orientale* reveal the existence of delicate squamules, of which a pair is associated with the base of each pedicel (Fig. 2, A, p. 15). These

structures, which I have also found in a number of other Crucifers, will be considered later (pp. 25–27).

Fig. 2, C, shows the general constitution of the flower of *S. orientale*. At their bases the inner stamens are united in pairs. In Fig. 2, D, a transverse section of a filament is drawn to show that

Fig. 2. *Sisymbrium orientale*, L. A, transverse section of young inflorescence axis to show squamules associated with a very young pedicel (× 37). B_1–B_7, series of transverse sections from below upwards through a fruit (× 37) from B_1 (receptacle below fruit) to B_7 (through loculi and two funicles whose ovules are not shown in this section). For further description see text, pp. 15, 16. C, transverse section of flower-bud (× 37). D, transverse section of a stamen filament (× 154 *circa*).

its structure is amphiphloic. Xylem of rather open texture, occupying the centre of the section, is surrounded by a phloem zone, with discontinuous groups of delicate fibres on its outer margin.

The young fruit can be studied in a series of transverse sections in Fig. 2, B_1–B_7. In B_1, which is cut through the receptacle, the xylem of the bundles is alone represented, the elements being

indicated individually; in later figures the bundles are shown diagrammatically. In B_1 the four inner stamen bundles are seen passing out; the gaps which they leave break the vascular ring into two broader median segments, the replum systems, and two narrower lateral segments, the valve systems. In B_3, a horizontal plexus of strands has come into view, arising principally from bundles which belong to the replum system, but are adjacent to the median bundles of the valves. But the strand *x* in B_2, which is separated by a stamen gap from the replum system, plays a part in the formation of the plexus (B_3), which thus, though chiefly of replum origin, is partially of valve origin. In Fig. 2, B_4, the plexus bundles fuse across inside the valve bundles to make two arcs which unite into an ☓ in B_5. In B_6, the upright median limb of the ☓ is lost, and two arcs—the placental strands—are thus produced on the inner side of the replum strands. In B_7 branches from one of the placental strands are seen passing into two funicles. It will be recognised from this description that the placental strands, though ultimately taking up a place on the inner side of the replum bundles, do not belong exclusively to the replum system—the valve system also plays a part in their formation. Moreover, of the four valve laterals seen in B_7, three originate from the replum system and the fourth from the valve system.

(iii) *Raphanus sativus*, L.

In Fig. 3, A_1, p. 17, a flower of the Garden Radish is cut through the pouched bases of the outer sepals. A_2, which is slightly higher, shows that the gland supply strands arise mainly from the bundles at the margins of the gaps left by the outer stamen bundles, but that they also have connections with the petal strands. Each petal bundle gives off one lateral strand to each of the sepals adjacent to it; these connections are indicated by dotted lines in A_3. In this section it is also seen that two of the four vascular masses left by the outward passage of the inner stamens, have fused by their xylems and phloems across one of the gaps, and that a third is united to them by its phloem. A little higher, the two remaining gaps are closed by phloem bridges. Figs. 3. A_4–A_{11}, record the behaviour of the bundles after the inner stamens have separated from the base of the gynaeceum. In A_4, the vascular ring has broken up into separate bundles, and in A_5 and A_6, the four unlignified strands, x_1–x_4, flanking the valve bundles, are seen passing in towards the centre. In one case, instead of the whole bundle moving inwards, half (*x'*) remains in the outer

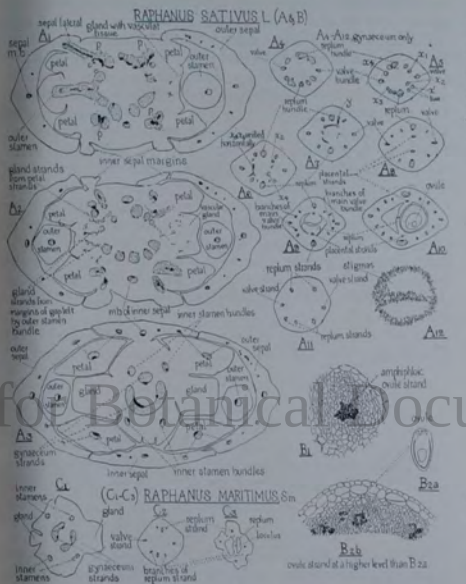


Fig. 3. *Raphanus*. A and B, *R. sativus*, L. A_1–A_{12}, sections from a transverse (slightly oblique) series through a flower from below upwards (× 28 *circa*). A_{12}, from five sections; *p*., vascular strands for petals. A_4–A_{12}, gynaeceum only. A_{12}, from more than one section. A_{11}, just below papillose stigma. For further description see text, pp. 16 and 18. B_1 and B_2, sections of an ovule from an unripe fruit. B_{2a}, transverse section of the amphiphloic strand at the back of an ovule (× 116). At a higher level, the bundle, after extending laterally, breaks up into the complex strand drawn in B_2, *a* and *b*. B_3 *a*, ovule (× 8 *circa*); B_3 *b*, vascular strand only (× 116). C, *Raphanus maritimus*, Sm. C_1–C_3, three transverse sections (× 28 *circa*) from a series through a gynaeceum; C_1, receptacle; C_2, level of loculi.

The gynaeceum of *Crambe* is unusual among the Cruciferae in consisting of two distinct segments, of which the lower, which is sterile, forms in the fruit a mere stalk for the upper fertile region. In Fig. 4, B, which represents a young gynaeceum from a flower, the segments are recognisable, though not yet differentiated markedly from one another. In the gynaeceum shown in the series of sections A_1–A_{11}, there is an ovule in the lower segment (A_7) as well as in the upper (A_8), but presumably that in the lower segment would fail to develop further. I can also confirm Hannig's statement(18) that there is a replum, which begins to extend across the cavity above the lower ovule. The existence of this lower ovule and of a replum indicates that Bentham and Hooker's description(11), "siliqua... articulo inferiore...aspermo, superiore...1-loculari," does not apply to the ovary at this young stage, which departs less from the usual Crucifer type. The method by which the cavity is closed at the "joint" above the lower ovule is shown in Fig. 4, A_8; the loculi are almost obliterated by the growth and tangential division of the parenchymatous cells of the ovary wall.

The four receptacular glands, which are in the orthogonal planes, are seen in surface view in Fig. 4, B, and in section in Fig. 4, A_1.

(vi) *Nasturtium officinale*, R.Br.

I have chosen the Watercress, *Nasturtium officinale*, as an example in which to illustrate the history of the individual bundles of the pedicel in their course through the flower. These bundles are numbered so that their progress can be followed from diagram to diagram. The pedicel is not radially symmetrical; in the flower under consideration it contains four bundles, of which the larger (1 and 2) are laterally placed (Fig. 5, *1*, p. 21). In the next section (Fig. 5, *2*) which passes through the pouched bases of the outer sepals, *bundle* 2 has divided into three branches. The central branch, after giving off a strand for the outer sepal, passes into the corresponding outer stamen. But *bundle* 1, on the other side, behaves differently. Here the same division into three takes place, but the central bundle passes bodily into the sepal, and does not contribute to the stamen above this sepal, which is supplied later by a branch arising through the meeting and fusion of two branches from the lateral strands of *bundle* 1; i.e. it is the lateral strands of the triad from *bundle* 1 which supply the outer stamen to the right, whereas the central strand of the triad from *bundle* 2 supplies the outer stamen on the left-hand side of the flower. It is unnecessary to describe the history of all the bundles

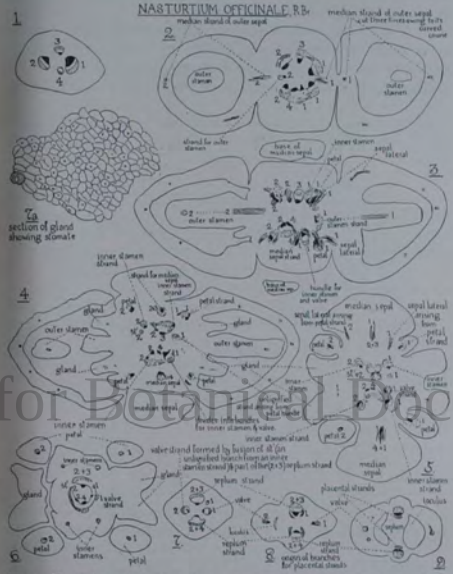


Fig. 5. *Nasturtium officinale*, R.Br. *1–9*, transverse sections from a series from below upwards through a flower (× 37, except *7 a*, which is × 154 *circa*). *1*, pedicel below flower; bundles numbered so that their history can be followed in successive sections. *2*, near flower-base; a section of the base of the downward curve of the outer stamen is seen in each sepal pouch. *3*, the outer stamen strand dips downwards before turning up into the filament, and is thus cut twice. *5*, outer sepals and outer stamens omitted. *6*, all sepals and outer stamens omitted. *7–9*, gynaeceum only. Fig. 6, C, p. 22, shows the stigmas for this flower; it would be number *10* of the present series. *7 a*, gland from level of 7, more highly magnified (× 154 *circa*). For further description see text, pp. 20–23.

in detail, since their paths can be traced in the diagrams. But the gynaeceum strands must be considered. When the four inner stamen bundles begin to move outwards (Fig. 5, 5), there are gaps where the valve bundles will eventually lie, though the position of the bundles supplying the replum is already marked out—2 and 3 nearest the median line to the north, and 2 and 4 nearest the median line to

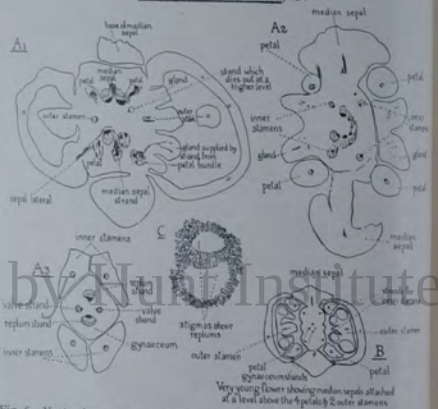


Fig. 6. *Nasturtium officinale*, R.Br. A_1–A_3, sections from a transverse series through a flower from below upwards (× 37). A_1, through pouches of outer sepals. A_2, outer sepals and outer stamens omitted. A_3, gynaeceum and inner stamens alone shown. B, transverse section of a very young flower to show late detachment of median sepals (× 37). C, transverse section of stigmas from the series drawn in Fig. 5, p. 21; this section is above Fig. 5, 9 (× 37).

the south. In Fig. 5, 6, an unlignified branch from an inner stamen strand, *st'*., fuses with part of the (2 + 3) replum strand to form one of the valve strands. The other valve strand, formed from 1, is also closely associated with an inner stamen strand. After the formation of the valve strands, the vascular tissue unites temporarily into an almost complete cylinder, but the identity of the bundles

is not lost. An asymmetric ground-plan after the outward passage of the inner stamen bundles is shown for another flower in Fig. 6, A_2, p. 22; this section may be compared with Fig. 5, 6. From Fig. 5, 7, onwards, the gynaeceum is represented alone. When we compare this figure with Fig. 5, 1, we see that *bundle* 1 has given one valve strand; *bundle* 2 has given the second valve strand, and also a portion to each replum strand; *bundles* 3 and 4 have each formed part of a replum strand. Fig. 5, 8, shows four horizontal branches, three of which are derived from the replum strands, while a fourth is the unlignified strand labelled 1 which arises from a petal bundle and can be traced through Figs. 5, 4–8. This strand is ultimately derived from that bundle in the pedicel (*bundle* 1) which plays no part in the replum system, but which supplies a valve strand. The four horizontal branches seen in 8 have fused in 9 into a single placental strand on the inner side of each replum bundle. We may thus conclude that in the flower of *Nasturtium officinale*, both valve and replum bundles are concerned in the formation of the placental strands.

The glands are seen in Figs. 5, 4–6, and one, on a larger scale, in Fig. 5, 7 *a*; it shows a stomate. In Fig. 6, A_1, a strand arising from a petal bundle is seen entering one of the glands and branching there; so far as my observations go, it is rare in the Crucifers to find gland strands so well developed as this.

(vii) *Lunaria rediviva*, L., and *L. annua*, L.

In Fig. 7, p. 24, I have illustrated the flower structure of *Lunaria rediviva*, a species specially notable for the high development of the gland supply strands. Fig. 7, A_1, shows the pedicel, which has the vascular asymmetry so often found in Crucifers. A_2–A_4 pass through the pouched bases of the outer sepals; in A_2 the basal cushions of the median sepals come into view. As in the other Crucifers described, each petal strand gives off two branches which form laterals for the sepals on either hand. The petal strand, after supplying these branches, is seen in A_2 *a* to pass through an amphiphloic stage below the level of detachment of the petal from the receptacle; by the time the petal is free, the bundle has become collateral. The concentric phase is shown on a larger scale in A_2 *b*. In A_6 we reach the base of the ovary, which is supplied by four bundles alternating with the four bundles of the inner stamens. It might naturally be supposed that these four bundles were the valve and replum bundles in their final form. But careful examination shows that this is not the case.

It will be seen that one of the valve strands (v_1) in A_6 is markedly wider than the opposite one (v_2). At a higher level, v_1 contributes a large part of itself to r_1, so that the north replum bundle in A_7

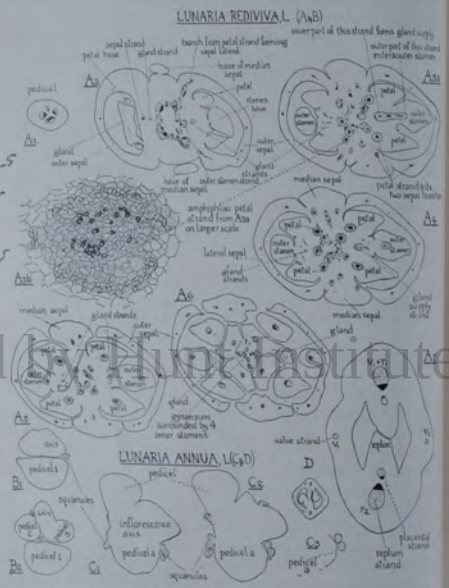


Fig. 7. *Lunaria*. A and B, *L. rediviva*, L. A_1–A_7, sections from transverse series through a pedicel and its flower (× 11, except A_3 *b* which is × 15 *circa*, and A_7, × 62 *circa*). For description see text, pp. 23–25. B_1 and B_2, transverse sections near the apex of an inflorescence axis to show pedicels and squamules (× 37). B_1, below B_2. C and D, *L. annua*, L. C_1–C_3, transverse sections from a series upwards from below near the apex of an inflorescence to show pedicels and squamules (× 37). D, transverse section of a young ovary (× 18).

is really compound. This diagram is on a larger scale than the others in order to show more clearly the inverted placental bundles. These are derived from the bundles external to them; the north placental bundle belongs, therefore, partly to the valve and partly to the replum system.

It will be noticed that the gynaecum of *L. rediviva* does not diverge much in sectional shape from the ordinary Crucifer siliqua, and the same point is still more clearly shown in the accompanying sketch of an ovary section of *L. annua* (Fig. 7, D). The expansion in the plane of the replum, which produces the characteristic seed-vessel of Honesty, is a later development.

In both *Lunaria rediviva* and *L. annua* there are only two glands, laterally placed; these glands in *L. rediviva* are developed both above and below the bases of the outer stamens, from which they receive their vascular supply. (For a description of the gland supply, see p. 30.)

The very young pedicels of *Lunaria rediviva* are associated at their bases with pairs of squamules (Fig. 7, B_1). These also occur in *L. annua*, and in this species they break up into separate setae. This process can be followed in the case of pedicel *a* in Figs. 7, C_1–C_3.

3. Discussion

(i) *The vascular ground-plan of the pedicel*

In examining serial sections of Crucifer inflorescences, one is immediately struck by the lack of radial symmetry in the vascular skeleton of the pedicel. This is illustrated for *Lunaria rediviva*, L., in Fig. 7, A_1, p. 24, and for *Nasturtium officinale*, R.Br., in Fig. 5, 1, p. 21. It seems generally to be due to a relatively poor development of the vascular tissue on the adaxial side of the pedicel, as will be recognised from the section of a young inflorescence of *Arabis verna*, R.Br., drawn in Fig. 8, A_1, p. 26. This tendency to dorsiventral symmetry brings the pedicels of the Crucifers into line with petioles rather than axes; it is an example of the anomalies encountered in the attempt to maintain a rigid morphological distinction between stem and leaf structures.

(ii) *The squamules associated with the pedicels and leaves*

The section of a lateral inflorescence of *Arabis verna*, R.Br., drawn in Fig. 8, A_1, p. 26, referred to in the previous paragraph in connection

also regarded the median sepals as the lowest. But serial sections show that the *lateral* sepals are actually the first of all the floral members, both in their detachment and in the origin of their median bundles; the sepals in the antero-posterior plane do not appear until a higher level. The early separation of the lateral sepals is seen, for instance, in Fig. 6, B, p. 22 (*Nasturtium officinale*); here the median sepals are not detached from the receptacle, even at a level at which the petals and outer stamens have already become free. The early origin of the midrib bundles for the outer sepals is seen in *Arabis albida*, Stev., Fig. 9, D_1, p. 31; *Nasturtium officinale*, R.Br., Fig. 5, 2, p. 21; *Sisymbrium Alliaria*, Scop., Fig. 1, *1–4*, p. 13. I doubt whether there are any Crucifers in which the bundles for the two pairs of sepals emerge *precisely* at the same level. It should be recalled that Klein (19) long ago maintained on anatomical grounds that the lateral sepals were in reality the outer. It is true that the margins of the lower lateral sepals are enclosed by those of the higher median sepals (e.g. *Sisymbrium orientale*, L., Fig. 2, C, p. 15). But Wydler was, I think, right in his contention that the sequence of floral members is not invariably revealed by their marginal relations; I have elsewhere touched on this point in connection with certain anomalies found among Bamboos ((7), p. 465). It seems to me that spatial as well as morphological considerations may determine how margins of foliar members shall overlap. The actual mode in which the margins of the median sepals of Crucifers come to enclose those of the earlier lateral pair can be followed for *Raphanus sativus*, L., in Fig. 3, A_1–A_3, p. 17. It will be seen from the diagrams that the marginal regions of the median sepals first come into view. Even before the median sepals are free from the axis, they have begun to enwrap the margins of the lateral sepals (A_2), but this does not alter the fact that the lateral sepals are the lower.

Special interest attaches to the question of which pair of sepals is in reality the lower, owing to a theoretical difficulty, to which attention has been called by Rendle (20). He points out that, according to Eichler's generalisation about the orientation of bracteoleless flowers ((16), p. 31), the absence of bracteoles in the Cruciferae should be associated with *lateral* placing of the two first floral members. But on Eichler's description of the Crucifer type, it is the *median* sepals which occupy the lowest place on the axis. This difficulty, however, ceases to exist when it is realised that—as I have shown—the lateral sepals are, in fact, the lowest floral members.

(iv) *The vascular relations of petals and sepals*

In 1894 Klein (19) describing the floral anatomy of *Matthiola* and *Cheiranthus*, stated that the petal bundles each divide into three below the base of the petal, and that the two side branches, instead of entering the petals, form laterals for the sepals on either hand. This description seemed to me so peculiar as to need confirmation, so I have examined the vascular relations of sepals and petals in a number of Crucifers. The result has been to show that Klein was entirely right, and moreover that his description can be extended to other species. I have followed the connection of petal and sepal strands in detail in *Cheiranthus Cheiri*, L.; *Lunaria rediviva*, L.; *Capsella Bursa-pastoris*, Medic.; *Sisymbrium Alliaria*, Scop.; *Rapistrum Linnaeanum*, Boiss.; and less fully in other Crucifers. And I now have little doubt that Klein's scheme holds good in general for the family. The process can be understood from several of my diagrams. In Fig. 1, 3, p. 13 (a section of a flower of *Sisymbrium Alliaria*, Scop., at a level below that at which the petals become free) the petal strands, and the sepal laterals to which they give rise, are connected by dotted lines. And in Fig. 3, A_3, p. 17, I have indicated—again by dotted lines—which of the sepal bundles of *Raphanus sativus*, L., originate from the petal strands. Those who wish to bring these facts into line with more orthodox views, may perhaps suggest that the sepal laterals really belong to the median strands of the sepals, but that they form a temporary union with the petal strands during their outward passage. But that such an interpretation is unfounded is shown by the series of sections through a flower of *Nasturtium officinale*, R.Br., drawn in Fig. 5, p. 21. It is clear from Fig. 5, 3, etc., that the petal strands are, in their origin, not even adjacent to the median strands of the sepals, but are separated from them by vascular tissue which has other destinations. The branches from the petal strands which enter the sepals as laterals, are thus wholly petaline in origin, and have no connection at any level with the median bundles of the sepals.

The vascular relations of petals and sepals outlined above, are of some theoretical importance. As Čelakovský (15) pointed out in reference to Klein's work, the anatomical method, carried to its extreme, would land us in the *reductio ad absurdum* of regarding the marginal regions of the Crucifer sepals as of petal nature. Indeed, the logical deduction from Klein's observations seems to be that vascular bundles are perfectly capable of disregarding morphological

boundaries. It is necessary to bear this in mind, for in some recent work the vascular system is treated as though it were provided by nature to serve as a clue in morphological labyrinths.

(v) *The glands and their vascular supply*

In the Crucifers, the glands in the neighbourhood of the stamen bases are variable both in number and arrangement; a few of the forms in which they may appear are illustrated in my diagrams. Fig. 9, F, p. 31, shows the six glands of *Lepidium draba*, L.—two at the base of each outer stamen, and one between each pair of inner stamens. The number of glands may exceed six, but is frequently less. Fig. 4, B, p. 19, is an external view of a gynaeceum of *Crambe maritima*, L., with four glands below it in the orthogonal planes; these glands are seen in section in Figs. 4, A_2 and A_3. *Lunaria rediviva*, L., has two glands (Fig. 7, A_4, p. 24); when the glands are as few as two they are generally associated with the lateral stamens only. The glandular tissue in some cases forms a continuous zone round the axis, so that the boundaries between the individual glands cannot be sharply defined, e.g. *Sisymbrium Alliaria*, Scop., Fig. 1, 6, p. 13. In this species the bases of the outer stamens are completely surrounded by glandular tissue; if the gland to the right is followed, it will be seen below the stamen in Fig. 1, 4; on either side of it in 5 and 6; and above it in 7.

The glands are parenchymatous. The epidermis is not, as a rule, markedly different from the underlying tissue, but in *Iberis amara*, L. (Fig. 9, C, p. 31) and *Hexaptera pinnatifida*, G. et H., I have found it to be columnar. Fig. 5, 7 *a*, p. 21, shows a stomate or water pore in the gland epidermis of *Nasturtium officinale*, R.Br. The glands are supplied by extremely delicate vascular strands; these strands have no xylem, but consist exclusively of elements with the characters of protophloem. The slight development of the strands and their lack of lignification, make it difficult to trace them to their source. In the species in which I have succeeded in following them, I have found a surprising lack of uniformity in their origin. To make this clear, I will now summarise, with certain additions, the facts about the gland supply recorded in the descriptive section of this paper.

In *Arabis albida*, Stev. (Fig. 9, D_1 and D_2, p. 31) each of the glands on the radius of the outer stamens is supplied by delicate strands from the median bundle of the outer sepal. These fibrils arise from the upper surface of this bundle, in the region where it curves over into the basal pouch of the sepal. In *Cheiranthus*

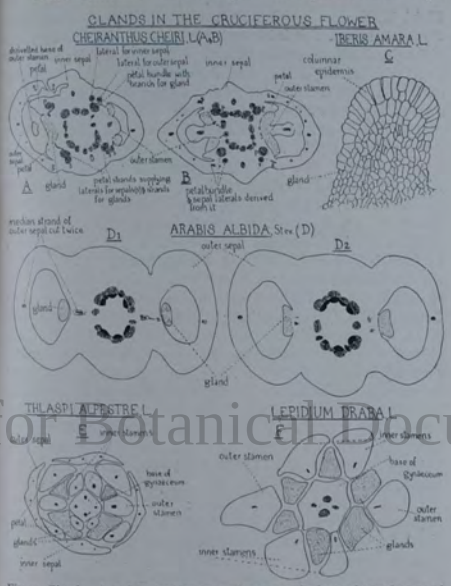


Fig. 9. Glands. A and B, transverse sections near the base of two flowers of *Cheiranthus Cheiri*, L. (× 18); *p.*, petal strand; *s.*, sepal laterals. A, drawn from ten sections to show vascular supply for all four glands. The series is slightly oblique, so that the right-hand side is cut at a slightly lower level than the left. B, section of another flower at about the same level as A; slightly oblique, so that the right-hand side is cut at a slightly higher level than the left. C, *Iberis amara*, L., gland from transverse section of a flower (× 154 *circa*). This gland was one of the two lying to either side of an outer stamen, and the orientation is thus at right angles to that of the other figures. D, *Arabis albida*, Stev., two transverse sections of a flower through the pouches of the outer sepals (× 37); D_1 below D_2. E, *Thlaspi alpestre*, L., transverse section of a flower (× 37); section slightly oblique, so that the north side is cut at a higher level than the south side. F, *Lepidium draba*, L., transverse section passing through the base of the ovary (× 37).

connected with the hindrance to the further flow of sap when the distal region of the organ is approached.

The interpretation of the gynaeceum has been much confused in the past by a tendency to treat the stigma as if it were a separate morphological entity. But if the orthodox foliar view of the carpel is valid, the stigma is merely an upward prolongation of some part of the carpellary leaf (or leaves). A feature of the Cruciferous gynaeceum which has been held to present a difficulty is the position

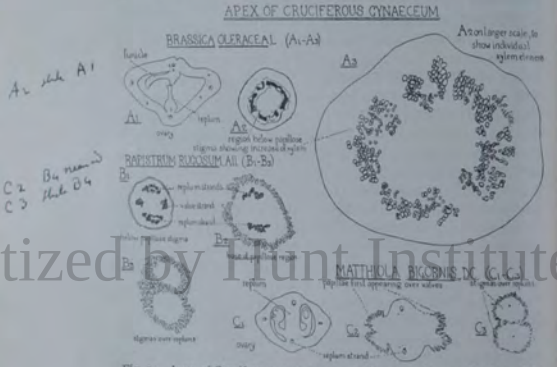


Fig. 10. Apex of Cruciferous gynaeceum. A, *Brassica oleracea*, L., A_1 and A_2, transverse sections through ovary and above (× 18). A_3, section drawn in A_2 (× 62 *circa*); individual xylem elements indicated. B_1–B_3, *Rapistrum rugosum*, All., three sections from below upwards through the stigmatic region (× 37). C_1–C_3, *Matthiola bicornis*, DC., three sections from below upwards through ovary and stigmas (× 37).

of the stigmas, which are situated, not over the midribs of the valves, but over the replums (Fig. 10, B_1–B_3). Even the stigmas of *Matthiola* (Fig. 10, C_1–C_3) do not depart essentially from this type, though this genus is sometimes spoken of as though it formed an exception. On the bicarpellary view, stigmas over the replums ("commissural") are regarded as a continuation of the fused margins of the carpels; it has been claimed as one of the recommendations of the quadricarpellary theory that it does not involve this idea

of marginal stigmas. But why need this idea be avoided? That in certain stigmas the carpel margins should play a predominant rôle need not surprise us, when we remember that the main feature of the carpel, as originally defined by de Candolle(14), is the development of ovules on the *margin* of the leaf. This promotion of the leaf-margin to an entirely new status, constitutes a fundamental difference from the foliage leaf, in which the midrib is, as a rule—though not invariably[1]—the most important region. There is thus no *a priori* difficulty in the continued upward growth of the carpellary margins to form stigmas. The doubleness of the replum bundle in certain Crucifers, or its bifurcation in the upper region (e.g. *Sisymbrium Alliaria*, Scop., Fig. 1, 9 and 10, p. 13) may well be claimed as an indication that it is a compound structure, formed—as the bicarpellary view postulates—by the fusion of the marginal bundles of two carpels.

(c) *The vascular analysis of the gynaeceum.*

The recent revival of the old 4-carpellary view of the Crucifer gynaeceum claims to be based primarily on anatomy(21–24). The assumption that the number of vascular bundles in the base of the ovary is an absolute guide to the number of carpels, is treated as axiomatic(23), and no proof of it is offered; it is even referred to as "the 'one cord to each carpel' rule." But I wish to point out that this "rule" has no claim to rank as an *axiom*; it is an *hypothesis* which ought not to be accepted without proof. As a comment upon it, it may be recalled that when four bundles enter the base of the gynaeceum in the Cruciferae, these four bundles are not always identical with the two valve and two replum bundles observable higher up in the ovary, though they might appear to be so if hand-sections alone were employed. *Crambe maritima*, L., is interesting from this point of view. In Fig. 4, p. 19, I have labelled as *A*–*D* the four bundles left after the outward passage of the four inner stamen strands. A process of division and fusion, which can be followed in Figs. 4, A_2 and A_3, results in *A* providing both one whole valve bundle and one whole replum bundle; *D*, one whole replum bundle; *B* and *C* together, one valve bundle. And in *Lunaria rediviva*, L., I have observed a similar state of affairs. In the flower illustrated in Figs. 7, A_1–A_7, p. 24, the four strands (A_6) left by the exit of the inner stamen bundles do not all behave alike. One becomes a valve strand, and a second becomes a replum strand, but the third divides, part of it becoming the second valve strand, while the other part fuses with the fourth

[1] For exceptions see (6), p. 77.

STUDIES IN FLORAL MORPHOLOGY

II. ON SOME NORMAL AND ABNORMAL CRUCIFERS: WITH A DISCUSSION ON TERATOLOGY AND ATAVISM

BY

AGNES ARBER, M.A., D.Sc.

FROM THE NEW PHYTOLOGIST, VOL. XXX, NO. 3, 1931

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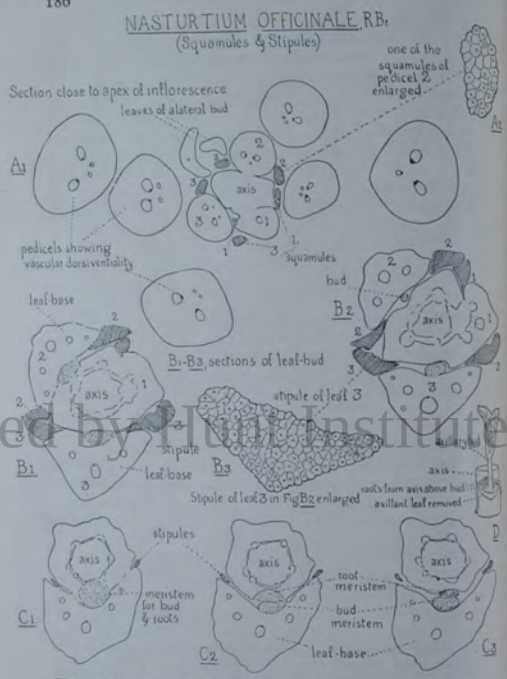

Fig. 8. *Nasturtium officinale* R.Br. Squamules and stipules. A_1, transverse section close to the apex of an inflorescence (× 92 circa) to show pedicels with their dorsiventral vascular scheme, and the squamules (shaded) associated with the three youngest leaves, 1, 2, 3. A_2, one of the squamules of leaf 2, enlarged further (× 232 circa). B, two sections, B_1, below, and B_3, above (× 56 circa) from a transverse series through a leaf-bud to show stipules (shaded) which are attached in B_1 and free in B_3 (× 232 circa). C_1–C_3, sections from a transverse series from below upwards (× 28 circa) through a leaf-bud (stipules shaded) to show origin of a lateral bud and its associated roots. D, segment of axis, enlarged, from which an axillant foliage leaf has been cut away, to show the axillary bud with its associated roots arising from the surface of the internode above it.

+ This had been already worked out by Norman, J.M. (1858) Lin Mpk Obs (11) 39

Crucifers, and I suggested that these squamules represented the stipules for the non-existent bracts.* Some illustrations of the squamules and stipules of *Nasturtium officinale* R.Br., are added here (Fig. 8, p. 186), since a study of this species, in which they are unusually well-developed, confirms the suggested interpretation. Fig. 8, A_1, shows a section close to the apex of a young inflorescence. The squamules (shaded) are seen in association with the youngest leaves, marked 1, 2, 3. In A_2 one of the squamules is drawn on a larger scale. B_1–B_3 show the stipules of a foliage leaf for comparison. They consist of parenchyma cells densely filled with cytoplasm. The stipules are on a larger scale than the squamules, but otherwise these structures resemble one another. It is not difficult to see how absence of the main body of the leaf might bring the stipules into intimate relation with an axillary axis—the pedicel—and thus give rise to that close association of "squamules" with the pedicels, which we see in the inflorescence. C_1–C_3, which are on a smaller scale, show the reduced importance of the stipules in the case of a somewhat older leaf. These structures are ephemeral—shrivelling and disappearing altogether at an early stage—so that, for systematic purposes, the leaf may still be described as "exstipulate."

Fig. 8, C_1–C_3 and D, incidentally illustrate the special relation of axillary buds and adventitious roots observable when shoots of Watercress are examined with the naked eye. Each axillary bud is accompanied by roots, but these arise from the main axis just above the bud, and not from the bud itself (D). In C_1, it will be noticed that, opposite the median bundle of the leaf-base, a meristematic area, elliptical in section, extends from the vascular ring of the axis, into the leaf. This area has divided in C_2: the inner segment remains at this level as part of the axis, while the outer portion is in process of detaching itself both from leaf and axis. In C_3, the inner segment of the meristem, while still attached to the axis, has divided into three root rudiments, side by side, while the outer part, which is completely detached, is the axillary bud.

(ii) *Abnormality with accessory flowers*

Late in June, 1929, I found, near Cambridge, fruiting racemes of the Watercress, *Nasturtium officinale* R.Br., in which some of the lowest flowers had evidently been abnormal, for the receptacle below each siliqua bore the remains of from one to four small supernumerary flowers. Fig. 9, B, p. 188, shows the general appearance of such an anomalous raceme ($\frac{3}{8}$ natural size), while Fig. 9, C, represents a

cf Atelanthera wrt Goebel 1933
Cardamine Chenopodifolia
Fg 1934 pp
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STUDIES IN FLORAL MORPHOLOGY

III. ON THE FUMARIOIDEAE, WITH SPECIAL REFERENCE TO THE ANDROECIUM

BY

AGNES ARBER

FROM THE NEW PHYTOLOGIST, VOL. XXX, No. 5, 1931

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STUDIES IN FLORAL MORPHOLOGY 6

IV. ON THE HYPECOIDEAE, WITH SPECIAL REFERENCE TO THE ANDROECIUM

BY

AGNES ARBER

FROM THE NEW PHYTOLOGIST, VOL. XXXI, No. 3, 1932

CAMBRIDGE
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ARBER, AGNES.

STUDIES IN FLOWER STRUCTURE.
I. ON A PELORIA OF DIGITALIS PURPUREA, L.

[Annals of Botany, Vol. XLVI, No. CLXXXIV, October, 1932.] Printed in Great Britain.

flower-bud. A_1 and A_2 show the base of the flower and the detachment of the calyx. The stamen whose bundle is marked with an asterisk in A_4,

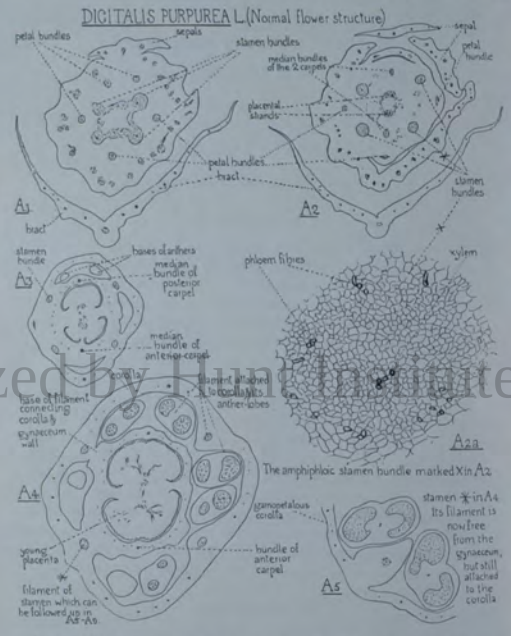

FIG. 1. *Digitalis purpurea*, L. Structure of normal flower, garden material. A_1–A_5 (and A_6–A_9, p. 931), transverse sections from a series from below upwards through a flower-bud; A_1–A_5 (× 16 circa); $A_2 a$ (× 218 circa); A_4 and A_5 (× 26 circa). In A_2 the outermost sepal was broken and is slightly reconstructed. $A_2 a$, the stamen bundle × in A_2, more highly magnified. In A_1 and A_4, bract and calyx omitted. The series through the stamen marked * in A_4 is continued in A_5 and in Fig. 2, p. 931.

is traced upwards in A_5 and in Fig. 2, A_6–A_9, p. 931. In A_7 it is noticeable that not only the filament, but each anther-lobe, has a vascular bundle.

A1. K7. I-5
A2 K6 meth
A3 K6 -II.10
A4 K6
A5 K6.II-7

The septum between the two pollen-sacs of each lobe is remarkably massive, and protrudes into the sac, so that the archesporium is kidney-shaped in

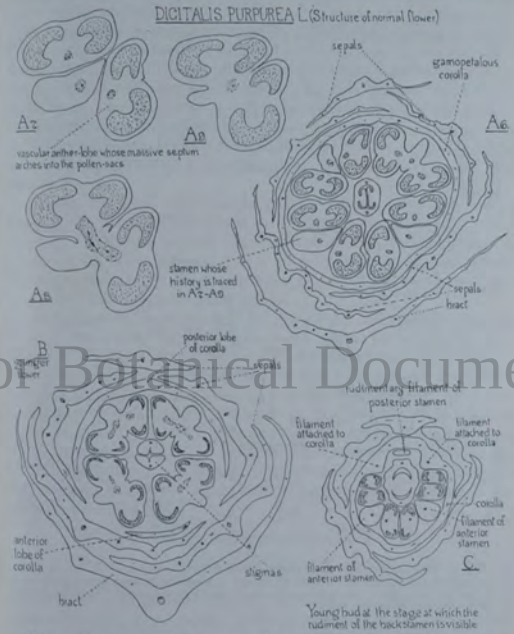

FIG. 2. *Digitalis purpurea*, L. Structure of normal flower, garden material. A_6–A_9, continuation of series drawn in Fig. 1, p. 930, A_6 (× 16 circa), A_7–A_9 (× 26 circa). B, transverse section of another younger flower-bud (× 26 circa), cut through the level of stigmas and anthers. A rudiment of the missing posterior stamen was visible at a lower level. C, transverse section through a flower-bud younger than B (× 26 circa) to show rudimentary filament of the missing posterior stamen.

section. This feature is shown still more strikingly in Fig. 2, B, which represents a younger flower; the septa are exaggerated to such a degree

A6 K5-II-6
A7 K5-III-7
A8 K5 II-6
A9 K5-II-6
B L.13.-I 6
C L12.II5

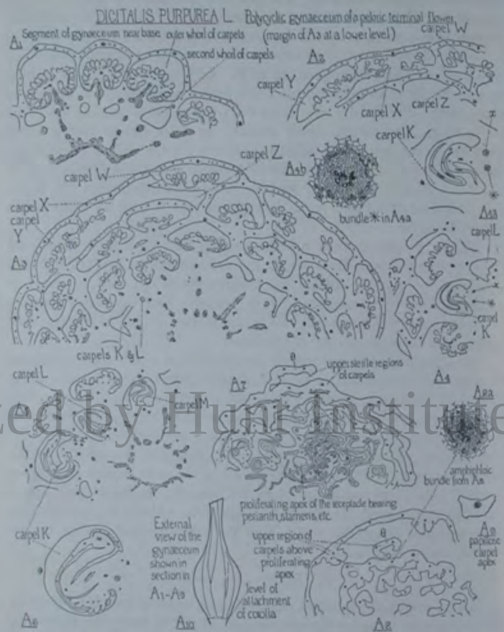

FIG. 4. *Digitalis purpurea*, L. Gynaeceum structure of first peloric flower, Nailsea, June 1928. The gynaeceum as a whole is shown in A_{10} (× 4/5 circa). A_1–A_9 are from transverse sections from below upwards through this gynaeceum, and the proliferation internal to it. Owing to its size, it had to be cut into segments before microtoming, with the result that the orientation is not consistent, except within the series A_2–A_6, and between the two sections A_7 and A_8. A_1 (× nearly 8), part of a section near the base of the ovary. A_2–A_6, series through a part of the gynaeceum, above A_1 (× nearly 8, except A_4a and A_6, × 13 circa, and A_4b, × 109 circa). The carpels K, L, X, Y, Z are lettered in order that their changes of structure in passing up may be followed more easily. A_7 and A_8, higher in the gynaeceum, above the level of the ovary (× nearly 8). The relation of these two diagrams can be understood from the position of the letter θ, which marks a corresponding point in both; the outermost carpellary wall is omitted in A_7, but shown in A_8. A_8a, median bundle of carpel (× 109 circa). A_9, one of the carpels near the tip of the gynaeceum (× 13 circa).

A1. IA. 21 A2 B1 A3 IB4
A4 IB8 A5. IB11. A6 IB15 A7. IC13
A8. IC1 (C19)7 A9. C6 = C24

empty basal regions. A_2–A_6 is a series through a higher part of the gynaeceum than that shown in A_1; this series indicates the changes which

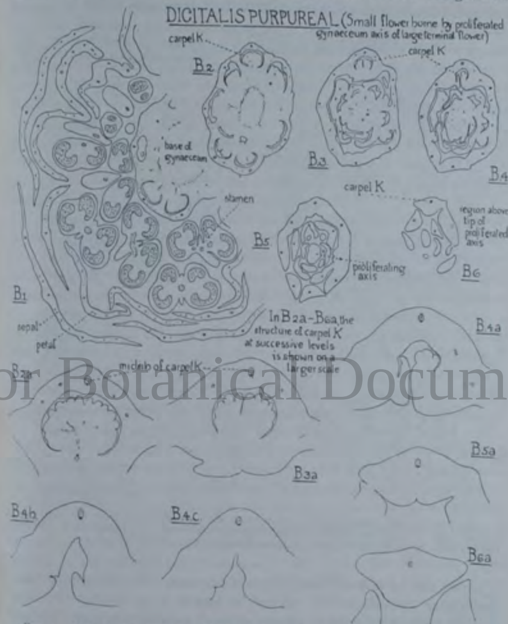

FIG. 5. *Digitalis purpurea*, L. Structure of a small apical flower from the second peloria, Nailsea, 1928. B_1–B_6, sections from a transverse series from below upwards through the flower (× 15 circa); except in B_1 the gynaeceum alone is shown. B_2a–B_6a, larger diagrams (× 53 circa) in which carpel K in B_2–B_6 can be followed more easily. B_2a, B_3a, B_4a, levels of B_2, B_3, and B_4; B_4b, B_4c, levels between B_4 and B_5; B_5a, between B_5 and B_6; B_6a, above B_6.

occur in the placentae of the individual carpels between their basal and distal regions. A_3 is a section of half the ovary, giving a general idea of its configuration. It will be seen that the carpels form four concentric series, whereas Massalongo's specimen showed three only. It is probable

B1 IV 5 – I6
B2 IV 4 lower
B3 IV 4 II 3
B4 IV. 3. – II
B5 IV. 3. – II – 1
B6 IV 3 I – 2

that these series represent four whorls, but they are somewhat irregular, and it would perhaps be possible to interpret the carpels as spirally arranged. Three of the outer carpels (X, Y, Z) form one cavity in A_3, but

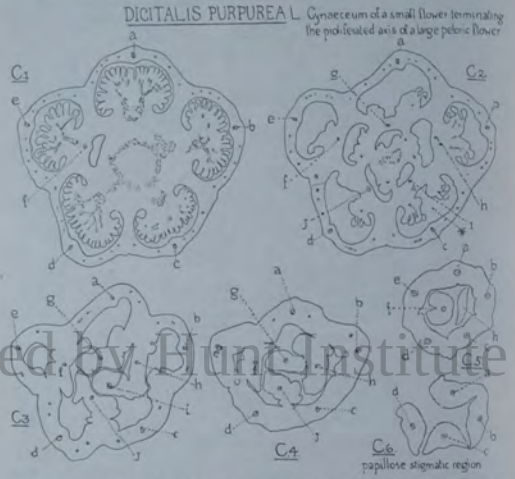

FIG. 6. *Digitalis purpurea*, L. Structure of small apical flower from the third peloria, Nailsea, 1928. C_1–C_6, transverse series from below upwards through the gynaeceum (× 26 circa). The five fully developed outer carpels are lettered *a–e*, and the five inner carpels *f–j*.

A_2 shows that at a lower level they are separate. The history of two of the higher carpels, K and L, can be traced in A_2 to A_6; the duplex character of the placenta is clearly defined, especially in A_4a. In A_6, one of the margins of carpel K is bearing ovules, while the other has suffered an abnormal leafy development. A_7 and A_8 are sections higher in the gynaeceum, above the ovary region. The relation of these two diagrams can be understood from the position of the letter *θ*, which marks a corresponding point in both; in A_7 the outermost carpellary wall is omitted. In this section the flattened upper regions of the carpels are still more or less fused with one another. This section shows a feature which is common to the six pelorias examined—the proliferation of the axis. The uppermost

C1. II 2 – II 10
C2. II 3 IV 4
C3 II 3 – II 6
C4 II 3 last one 7
C5 II 4 III 2
C6 II 4 – II 9

carpels are succeeded by a few abortive stamens, and then a series of perianth members, followed by more stamens, in which malformations are frequent. Above these, the axis produces some rudimentary leaf members, and then dies out. This proliferated tip of the axis was entirely enclosed within the gynaeceum, and its existence was not suspected until the gynaeceum was sectioned. A_8 is cut at a level above the tip of the proliferating axis, and thus shows only the carpels, which are now separating and revealing their one-bundled character. The median bundles of the carpels are bicollateral below, but at the level of A_8 they are all amphiphloic (cf. A_9a). The two amphiphloic bundles, *x'* and *x''* in A_5, have arisen by division of the amphiphloic marginal bundle of carpel K, marked *x* in A_4 and A_4a. A_9 represents one of the carpels near the tip of the gynaeceum, to show the papillose character of its inner surface.

A second peloric terminal flower from Nailsea was cup-shaped, and had nineteen stamens. The stamens were followed by a gynaeceum resembling that shown in Fig. 4, A_{10}, but the proliferation of the floral axis was carried further. It was prolonged as a leafy shoot terminating in a small flower, whose structure is illustrated in Fig. 5, p. 935. B_1 shows part of a transverse section through this flower. The petals are free for most of their length, but at, or just below, the base of the gynaeceum they are connected with one another, and with the stamen bases and the receptacle. Except in B_4 the gynaeceum alone is shown. The outer whorl consists of about seven ovule-bearing carpels (B_2). These are succeeded by a number of leafy structures borne by the proliferated axis of the gynaeceum (B_5 and B_6). In B_5a to B_6a carpel K is traced from below upwards.

A third inflorescence from Nailsea terminated in a flower with a large irregular cup-shaped corolla, with inner lobes that may have been staminal. There were twelve stamens. In place of a gynaeceum the axis emerged in the centre of the peloria, bearing a number of bracts, some green and some partially petaloid; it terminated in a small flower whose gynaeceum is shown in a series of sections in Fig. 6, p 936; in these sections the median bundles of the carpels are lettered *a–j*. In C_1 the five fully developed outer carpels (*a–e*) are seen, and one of the inner carpels (*f*). In C_2 the cavities of the five inner carpels (*f–j*) have come into view. These are succeeded by a few more leafy structures, above which the axis dies out. C_5 is cut above the tip of the axis, so that only the carpels are visible. In C_6 the five outer carpels are united by their margins, forming a continuous ring. Four of the five outer carpels, but none of the inner carpels, reach to the level of C_6.

III. Discussion.

I will not now attempt to discuss the meaning of peloric organization in general, since this is a subject which I hope to review in a later paper.

FLORAL ANATOMY AND ITS MORPHOLOGICAL INTERPRETATION

BY

AGNES ARBER

FROM THE NEW PHYTOLOGIST, VOL. XXXII, NO. 3, 1933

CAMBRIDGE
AT THE UNIVERSITY PRESS

PRINTED IN GREAT BRITAIN

(11) CANDOLLE, A. P. DE. *Organographie végétale*. Paris, 2 vols. 1827.
(12) DARWIN, C. *On the various Contrivances by which...Orchids are Fertilised by Insects*. London. 1862.
(13) EAMES, A. J. and MACDANIELS, L. H. *An Introduction to Plant Anatomy*. New York. 1925.
(14) GOETHE, J. W. VON. *Versuch die Metamorphose der Pflanzen zu erklären*. Gotha. 1790.
(15) GRÉLOT, P. Recherches sur le système libéroligneux floral des gamopétales bicarpellées. *Ann. d. Sci. Nat.* sér. viii, **5**, 1–154. 1897.
(16) HANSEN, A. *Goethes Metamorphose der Pflanzen*, **1**, text, **2**, atlas. Giessen. 1907.
(17) HENSLOW, G. *The origin of Floral Structures*. London. 1888.
(18) —— On the vascular systems of floral organs. *Journ. Linn. Soc. Bot.* **28**, No. 192, 151–97. 1890.
(19) RUSSELL, E. S. *The Interpretation of Development and Heredity*. Oxford. 1930.
(20) SARGANT, E. A theory of the origin of Monocotyledons. *Ann. Bot.* **17**, 1–92. 1903.
(21) SAUNDERS, E. R. On carpel polymorphism. I. *Ann. Bot.* **39**, 123–67. 1925.
(22) —— On carpel polymorphism. V. *Ann. Bot.* **46**, 239–88. 1932.
(23) THOMAS, H. HAMSHAW. The early evolution of the angiosperms. *Ann. Bot.* **45**, 647–72. 1931.
(24) THOMPSON, D'ARCY W. *On Growth and Form*. Cambridge. 1917.
(25) TIEGHEM, P. VAN. Recherches sur la Structure du Pistil et sur l'Anatomie comparée de la Fleur. *Mém. prés. par div. Sav. à l'Institut de France*, **21**, 2 vols., text and atlas. 1871.
(26) —— Sur l'existence de feuilles sans méristèles. *Rev. Gén. de Bot.* **8**, 481–90. 1896.
(27) TROLL, W. Organisation und Gestalt im Bereich der Blüte. *Monographien aus dem Gesamtgebiet der Wiss. Bot.* **1**. Berlin. 1928.

Saunders, E. R. Comments on "Floral Anatomy & its Morphological Interpretation". New Phyt. Vol 33, 1934 pp 127–170

not worth annotating in detail. the last sentence in the book better to stress letter to Nature, on the chance ... other examples of persistence of the trace ... bundle of a bract stamen which is lost — e.g. Ruellia pulchella Schott or R. formosa ... accurate. But the Andr. — ... evidence ... does not ... meristome ... use.

McLean Thompson I. 1924. p 33 describes the occurrence of a residual bundle representing the posterior stamen of Amherstia nobilis ...

Morphological Interpretation of Floral Anatomy

In the recent issue of the *New Phytologist*[1], Mrs. Agnes Arber, in a paper dealing with the above subject, raises certain points which are of fundamental importance to all plant morphologists. She discusses the use of anatomical evidence in phylogenetic morphology and comes to conclusions which are directly opposed to one of the well-established doctrines of modern comparative morphology. To the question, "Are we to consider it proven that the vascular bundles are more 'conservative' than the external form, so that vestigial organs may be represented by their bundles, when all external trace of these organs has disappeared", her answer is that "we have no alternative but to discard the doctrine of the conservatism of the vascular bundles". Proceeding further, she says, "there seems to be no escape from the conclusion that there is a complete absence of positive evidence for the vestigial survival of vascular tissue after the organ which it supplied has ceased to exist". She admits that the general nature of the vascular scheme may have a certain systematic value and may serve to some extent as an indicator of trends in race [illegible], but in her opinion "there appears to be no [illegible] for the statement of flowers that 'anatomical characters and *of the vascular system* are apt to tardily follow evolutionary progress and therefore to persist as vestigia" (italics mine).

Mrs. Arber appears to be partially right in this, especially because an unintelligent use of the above doctrine has sometimes led to the formulation of peculiar hypotheses, like the theory of carpel polymorphism, but her whole argument seems to be too much exaggerated. In her evidence she takes into consideration some highly specialised grasses, like *Luziola Spruceana*, Papaveraceæ like *Hypecoum* and *Corydalis*, and genera like *Antirrhinum* and *Digitalis*, on which she has happened to work. She has consulted some old works on the Primulaceæ wrongly interpreted by the previous authors and on the theory of solid carpel and carpel polymorphism, in which no one believes except its author, but makes no mention of some other recent works, especially from the United States. A reference to these would have shown her that evidence for the conservatism of vascular bundles is not so entirely lacking as she believes and that vestigial organs even in the flowers of angiosperms are represented in several instances by their vascular bundles. The Salicaceæ are an example. Fisher[4] has shown that the simplicity of the flowers of this family is largely due to extreme reduction, and a vestigial vascular supply is present in many instances to organs now greatly reduced or entirely lacking. During the study of the scheme, Chute[4] has found that sometimes there are abortive ovules without vascular supply, but in other instances an ovular trace is found to a suppressed ovule. Investigating the floral anatomy of the Urticales, Bechtel[5] finds in several species vascular traces of suppressed perianth leaves, stamens and carpels. In this order the carpel is mostly bicarpellary, but there is a great tendency to the suppression of one carpel. In some instances it almost becomes unicarpellate, but vestigial bundles are always present to show the existence of the second carpel. In some cases the inner whorl of perianth has entirely disappeared, in other instances vestiges of its vascular supply remain. In *Stellera Chamaejasme* (Thymelæaceæ), a plant I have studied, the corolla is entirely absent. There is, however, near the base of the flower a much reduced disc-scale. The vascular supply of this clearly indicates it to be a part of much reduced corolla.

All these examples are from the anatomy of the flowers of angiosperms, with which Mrs. Arber deals. As is well known, there are many more instances from other groups of vascular plants.

The position seems to be that it is not always essential for vestigial organs to be represented by their vascular bundles, but in many instances they are, and this seems to have been correctly stated by Bechtel in 1921. "In plant organs suffering reduction, the vascular system either disappears in advance of the organs, or persists as abortive bundles after the organs have disappeared."

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Oct. 1.

[1] Arber, A., "Floral Anatomy and its Morphological Interpretation", *New Phyt.*, **32**, 231 ; 1933.
[2] Bower, F. O., "The Ferns (Filicales)", vol. 1, Cambridge, 1923.
[3] Fisher, M. J., "The Morphology and Anatomy of the Flowers of Salicaceæ, I and II", *Amer. J. Bot.*, **15**, 307, 372 ; 1928.
[4] Chute, H. M., "The Morphology and Anatomy of the Achene", *Amer. J. Bot.*, **17**, 703 ; 1930.
[5] Bechtel, A. E., "The Floral Anatomy of the Urticales", *Amer. J. Bot.*, **8**, 386 ; 1921.

ARBER, AGNES

STUDIES IN FLOWER STRUCTURE

II. ON THE VASCULAR SUPPLY TO THE NECTARY IN RANUNCULUS

Reprinted from Annals of Botany
Vol. L, No. CXCVIII, April, 1936
Pages 305–320

Printed in Great Britain

basal structure of the petal, did not distinguish between scale and nectary; his statements will be discussed later (pp. 311–313). As no other description of the vascular supply for the nectary has been met with (see Postscript, p. 319), it has seemed that some account of it ought to be put on record.

2. Methods.

The vascular supply of the buttercup nectary is usually well preserved in flowers fixed in commercial methylated spirit. For examining the structure of the petal base as a solid object (Fig. 1, A, C, etc.), it was stained with alcoholic gentian violet, followed by eosin in oil of cloves to give translucency. There is a risk, in dealing in this way with a number of species, that a stray petal may get left behind, hidden by the dark staining fluid, and may then be mistaken for a petal belonging to some other species, which is passed through the stain later. For this reason I have found it best to carry entire flowers through the fluids, and not to detach the petals until the final xylol stage is reached. Preparations made in this way are useful for giving a general idea of the structure, but transverse microtome series are necessary if it is to be understood in detail. For these the modification of Fleming's triple stain devised by Sargant for anatomical work has been used: 1 per cent. Bismarck brown in 70 per cent. alcohol, followed by 0·3 per cent. aqueous gentian violet, differentiated with 1 per cent. aqueous orange G, followed by 1 per cent. orange G in 50 per cent. alcohol. Microtome series taken through whole buds or flowers are almost useless, because of the curvature of the petals and the angle at which they leave the receptacle; so it is best to cut off the basal regions of detached petals and embed them alone. For a complete treatment of the subject it would be necessary to keep the petals of each flower, and those occupying different positions within the same flower, separate in the paraffin, in order to see how the structural variation met with in the petals is related to the individuality of the plant or shoot, and to the topography of the flower. In the present slight sketch I have not attempted to do this, as it would have made it impossible to cover sufficient ground to give a general idea of the nectary supply in the genus.

Owing to the delicacy of the petals the nectary structure is not well preserved in herbarium specimens, so this study is based entirely on a few of the species, of which fresh or pickled material was available; and as the genus includes about 300 species (8), there may be many interesting variants which have been missed. In the following Section I have described my observations, leaving the general bearing of the work to be indicated briefly on pp. 316–318. The order in which the species are taken has been chosen merely for convenience in treating of the anatomy.

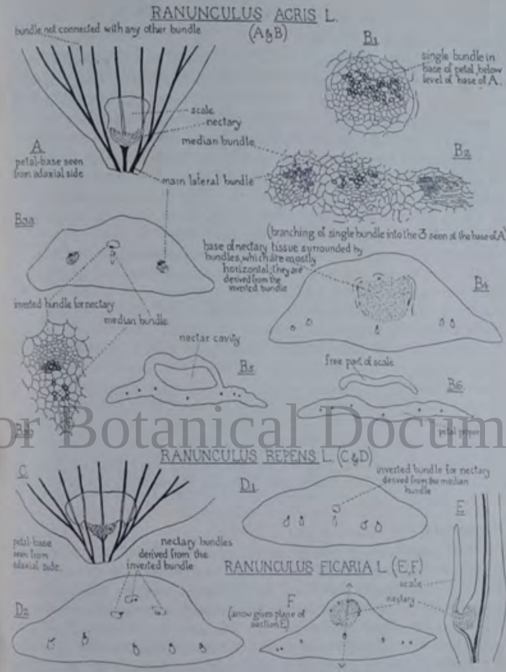

Fig. 1. Throughout the figures glandular tissue is dotted. In petal bases viewed as solid objects, the bundles are indicated in solid black except where they are seen faintly through the nectary scale. In sections, xylem is indicated in black and phloem in white. A, B, *Ranunculus acris* L. A, petal base viewed from adaxial side (× 14). B 1–B 6, sections from a transverse series from below upwards through a petal base; B 1, B 2, B 3 *b* (× 193 *circa*); B 3 *a*, B 4 (× 47); B 5, B 6 (× 23). B 3 *b* shows the median bundle in B 3 *a*, with its inverted branch, on a larger scale. C, D, *R. repens* L. C, petal viewed from adaxial side (× 14). D 1 and D 2, sections from a transverse series from below upwards through a petal base below the level of the nectary (× 47); lignified xylem elements indicated individually. E, F, *R. Ficaria* L. E, radial longitudinal section (× 23) of a petal base, in the plane marked with an arrow in F (semi-diagrammatic reconstruction from longitudinal series). F, sections from a transverse series through a petal passing through the base of the nectary (× 23); E and F being from different petals are not consistent in proportions.

Harston rumb July 14. 35. B1 cf C1; B2, C1 II-2; B3, C1 III-7; B4, C1-II-4; B5, C2 II 9; B6, C2 III-6 approx; D1, A2 I 10; D2, A2, III-2.
F. B2. IV-4. B series, outer free petals, 1935, also radial long sect.

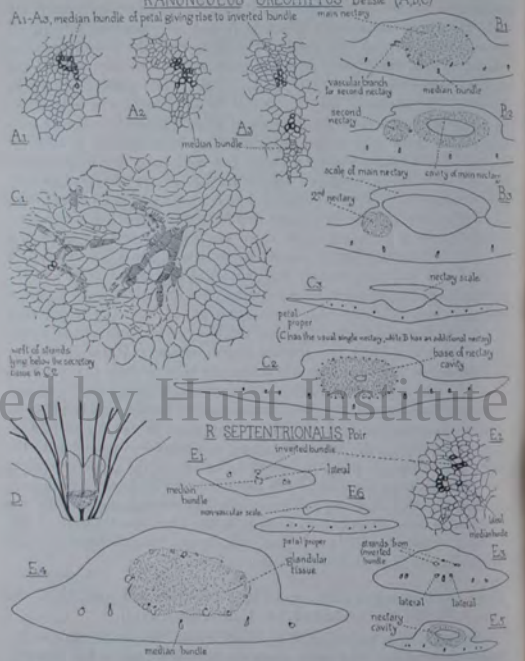

FIG. 3. A–C, *Ranunculus oreophytus* Delisle. A, B, sections from a transverse series, upwards from below, through one petal. A 1–A 3, origin of inverted branch from collateral median bundle (× 193 *circa*). B 1–B 3, median region of the petal (× 23); B 1, through main nectary below cavity; B 2, through main nectary in region of cavity; B 3 above glandular tissue of main nectary; B 2 and B 3 show second nectary. C 1–C 3, sections from a transverse series from below upwards through another petal base. C 2, through the base of the nectar cavity (× 23); C 3, through the free part of the scale (× 14). C 1 (× 193 *circa*) shows the weft of strands below the nectary at a lower level than C 2. D and E, *R. septentrionalis* Poir. D, petal base viewed from adaxial side (× 14). E 1–E 6, sections from a transverse series from below upwards through a petal. E 1, E 3 (× 23); E 2 (× 193 *circa*); E 4 (× 47); E 5, E 6 (× 14). E 2 shows the median bundle in E 1, and the two branches it is giving off for the nectary, on a larger scale.

A1-3. Median petal A sister. B1, A3 II-5; B2, A3-I-1
B3, A3-I 1. C1, C2-II 2; C2+C3, E2-I 6
E6, A3 I 6; E5, A2-I-4; E4, A2-II-6; E3, A2 II-9;
C2, A2 I-6; E1, A2 I 6

G. Hume Smith's account, and that the structure, in the examples which I was able to study, falls into line with that of other buttercups. In five petals, of which I cut transverse series, no strand, lignified or unlignified, rises into the free part of the scale. Moreover no lignified bundle penetrates even into the lower part of the scale where it is fused marginally with the petal surface; but a few delicate unlignified strands may rise for a short distance into this attached basal region of the scale. The origin of the vascular supply for the nectary in this species varies considerably, and is not so simple and diagrammatic as in some of the other buttercups. In the series illustrated in E 1–E 5, the median bundle contributes three strands which give rise to the nectary supply; one of these seems to correspond to the inverted bundle of *R. acris* etc., while the other two are lateral. In another petal there was no individual inverted bundle, but the median of the three main bundles gave off two laterals, each of which divided, thus forming a group of four bundles as the basis of the nectary supply. In another petal there was again no single inverted bundle, but the bundle given off for the nectary branched immediately in the horizontal plane.

R. pennsylvanicus L., Fig. 2, B, p. 310 (cult. Cambridge Botanic Garden).

As a contrast to *R. velutinus* and *R. septentrionalis*, in which the vascular system for the nectary is highly developed, *R. pennsylvanicus* may be noticed, as a species in which this system is much reduced. In three petals indications were found that a non-lignified bundle for the nectary was derived from the median bundle, but in two others no connexion was traceable between the slightly developed and non-lignified vascular system of the nectary and any of the petal bundles. It will be noticed in Fig. 2, B, that in the petal proper there are two marginal bundles, which do not run for the whole length of the petal, and which have no connexion, basally, apically, or by branching, with any other vein; they may be called 'free' bundles. Among eight petals, stained and mounted whole, I found in four, one free non-marginal bundle; in one, one free marginal; in one, one free marginal and one free non-marginal; in one (Fig. 2, B), two free marginal; in one, three free non-marginal. It is suggestive to find this discontinuity in the general vascular system of the petal, in a species which also tends to discontinuity between the main veins of the petal and the strands for the nectary; but it is not possible to lay much stress on this point, as free bundles of a corresponding type may occur in the general petal system of *R. acris* (Fig. 1, A) and *R. repens*.

R. gramineus L., Fig. 4, A–F, p. 314 (cult. Cambridge Botanic Garden).

Unlike the buttercups hitherto considered, in which the nectar cavity is bounded by an adaxial scale on one side and the upper surface of the petal on the other, *R. gramineus* belongs to the type in which the nectary occurs at the base of a tubular structure, which on the side towards the

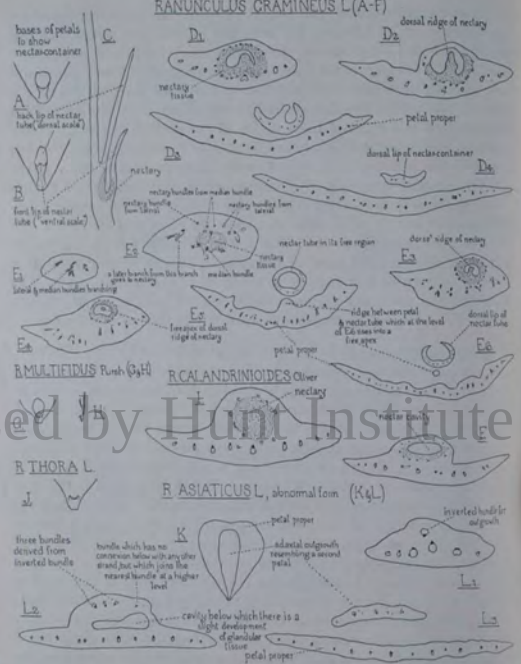

FIG. 4. A–F, *Ranunculus gramineus* L. A, B, bases of petals with honey tube viewed from adaxial side. In A, the length from base of petal to top of tube lip was just over 3 mm.; in B, 4 mm. C, radial longitudinal section of petal base, vascular tissue omitted (× 14). D 1–D 4, sections from a transverse series from below upwards through another petal base (× 23). E 1–E 6, sections from a transverse series from below upwards through another petal base (× 14, except E 2, × 23). F, transverse section of another petal passing through the nectar cavity (× 23). G, H, *R. multifidus* Pursh; G, petal base enlarged, viewed from adaxial side; length in this example from base of petal to tip of scale, 2·75 mm.; the scale is variable in size and form. I, *R. calandrinioides* Oliver, section from a transverse series through a petal base (× 23). J, *R. Thora* L., petal base viewed from adaxial side; in this example length from petal base to top of ridge, about 1 mm. K, L, *R. asiaticus* L., abnormal form, cult. Mr. G. P. Baker, 1930. K, duplex petal viewed from adaxial side (× 1½). L 1–L 3, sections from a transverse series through the base of a petal similar to K (× 14).

petal is continued upwards to form a free rim (the so-called 'dorsal scale'; see 8). Figs. A, B, C, show the external appearance and radial section of this nectar-container. There is a good deal of variation in its size and shape, but the figure given by Troll (14, Fig. 45, vii, p. 196) does not conform to the appearance of any of the flowers that I have examined. Some idea of the range of variation may be gained from Figs. D–F. In the series D the ventral lip of the nectar-container does not rise above the level at which the dorsal lip becomes free, so there is no free tubular region. There is a median ridge in the nectary tissue (D 1 and D 2) which is continued up into the free lip (D 3). In E, on the other hand, the ventral side of the lip is more developed, so that there is a free basal cylindrical region. The median ridge occurs here (E 3) as in D, and terminates in an isolated upward peg (E 4). A second peg-like outgrowth, which is not found in D, occurs between the back of the lip and the petal (E 5, E 6). In a third petal, whose nectary cavity is seen in section in F, there is no median ridge of nectary tissue, such as that seen in D and E. The vascular supply of the nectary in D, E, and F, is formed of components from the median bundle and the two main laterals (see E 2). There is so little lignification in the nectary bundles that their orientation cannot be determined.

R. asiaticus L., Fig. 4, K, L, p. 314 (cult. G. P. Baker, Sevenoaks).

Mr. Parkin tells me that in *R. asiaticus* 'in the wild form (dry material) the nectary is a basal shallow depression. In cultivated forms the nectary tends to disappear.' In May 1930 he kindly sent me four petals from a flower of a peculiar white form of this species, which he had received from Mr. G. P. Baker. These petals were duplex in character. An adaxial lobe, also white and looking like a second smaller petal, arose from the base of each (Fig. 4, K). In one case the length of the lobe was within 2 mm. of that of the petal proper. Sections showed that the bundles of this outgrowth had their xylems turned towards the xylems of the petal (L 1–L 3), the vascular scheme thus recalling the orientation of the main bundle for the nectary system in other buttercups. There was a slight but recognizable trace of glandular tissue at the base of the cavity between the petal and its outgrowth—so slight that it scarcely claimed any vascular supply. The small bundle to the extreme right of the inverted series in L 2 united at a higher level with the nearest bundle; basally it had no connexion with any other bundle, but it gave off a small branch which also ended blindly, and suggested a vestigial nectary supply. The meaning of the adaxial outgrowth, which is a curious feature in a species which does not normally possess a distinct ventral scale, will be considered on p. 317.

As an addendum to these observations it may be noted that serial sections of the petals of various species of Ranunculus often show—as might be expected—grains of pollen in the nectar-container.

by Thompson (13), this limitation may well lead to the production of further marginal upgrowths of various forms, giving the tube or 'dorsal scale' of the 'mat' buttercups.

(v) *The Predominance of Phloem in Nectary Supply Bundles.*

I have noticed elsewhere that in the vascular supply of floral nectaries in the Cruciferae, Fumarioideae, and Hypecoideae, phloem predominates (1, pp. 30–3; 2, pp. 342–3; 3, pp. 164–5). This is also true of Ranunculus. The relatively large amount of phloem in the inverted bundle, which will give the nectary supply of *R. acris*, is seen in Fig. 1, B 3 *b*. In all the buttercups which I have examined, the individual nectary strands, even if lignified at the base, terminate upwards in phloem alone. This seems to indicate that the carbohydrates in solution, which the gland uses for the manufacture of nectar, must travel—at least in the final stages of their journey—*via* the phloem.

So far as can be determined from microtome sections stained for general anatomy, the phloem tissue of the nectary supply consists entirely of cells of cambiform type, which often have elongated nuclei. A more complete histological study might, however, reveal greater complexity.

5. Summary.

In this paper the vascular supply to the petal nectary is described for the following species of Ranunculus:—*acris* L.; *repens* L.; *Ficaria* L.; *bulbosus* L.; *caucasicus* Bieb.; *velutinus* Tenore; *oreophytus* Delisle; *septentrionalis* Poir.; *pennsylvanicus* L.; *gramineus* L.; *calandrinioides* Oliver; and an abnormal form of *asiaticus* L.

It is shown that the nectary supply, in which phloem markedly predominates, is derived from the median bundle of the petal, often with the addition of components from the two main laterals. In the most typical of the 'glossy' buttercups the nectary branch, which arises ventrally from the median bundle, is inversely orientated, with its xylem facing the xylem of the median bundle. This inverted bundle may be regarded as the trace for the nectary scale, but since this trace is used up in supplying the nectary, the scale is left non-vascular in its free region. The idea that the scale is, despite its non-vascular character, an enation which follows the law of laminar inversion is confirmed by a study of a peculiar form of *R. asiaticus*, in which a reduced nectary is associated with an outgrowth resembling a hypertrophied ventral scale supplied by bundles of inverse orientation.

For material I am indebted to the kindness of Professor Edgar Anderson of the Missouri Botanic Garden, to Mr. G. P. Baker of Sevenoaks, to Mr. C. A. Weatherby, Curator of the Gray Herbarium, Cambridge, Massachusetts, and to the Curator of the Cambridge Botanic Garden. I must also express my gratitude to Mr. Parkin, not only for supplying me with flowers of the species of Ranunculus which he has under cultivation, but also for his constant help during the progress of this study and for criticism of the manuscript.

Postscript.

Since this paper was written I have found that I had overlooked two references which should have been included. The anatomy of the petal base in *Ranunculus acris* L. was described by G. Bonnier 'Les Nectaires. Ann. Sci. Nat., Bot., VI, viii, p. 102, Pl. 2, Figs. 16, 17, 1879'. E. J. Salisbury, 'On the Morphology and Ecology of *Ranunculus parviflorus* L., Ann. Bot., xlv, pp. 539–78, 1931' gives a photograph of a radial longitudinal section of the petal of this species, and writes, 'The petal is supplied by a single trace which passes to the base of the nectary, where it expands beneath the secretory tissue (Pl. XVIII, Fig. 4); from this expansion five slender strands are given off which pass into the limb of the petal.' (I have not found an example of this type of structure among the species which I have examined.)

Literature Cited.

1. Arber, A.: Studies in Floral Morphology. I. On some Structural Features of the Cruciferous Flower. New Phyt., xxx, 11–41, 1931.
2. ———: Ibid. III. On the Fumarioideae, with Special Reference to the Androecium. Ibid., xxx, 317–54, 1931.
3. ———: Ibid. IV. On the Hypecoideae, with Special Reference to the Androecium. Ibid., xxxi, 145–73, 1932.
4. ———: Studies in Flower Structure. I. On a Peloria of *Digitalis purpurea* L. Ann. Bot., xlvi, 929–39, 1932.
5. Brouland, M.: Recherches sur l'Anatomie florale des Renonculacées. Le Botaniste, xxvii, 1–252, 1935.
6. Čelakovský, L. J.: Teratologische Beiträge zur morphologischen Deutung des Staubgefässes. Pringsheim's Jahrb. f. wiss. Bot., xi, 124–74, 1878.
7. Kumazawa, M.: Studies on the Structure of Japanese Species of *Ranunculus*. Journ. Fac. Sci. Imp. Univ. Tokyo, III, Bot., ii, pt. 3, 297–343, 1930.
8. Parkin, J.: The Glossy Petal of *Ranunculus*. Ann. Bot., xlii, 739–55, 1928.
9. ———: The Structure of the Starch Layer in the Glossy Petal of *Ranunculus*. Ann. Bot., xlv, 201–5, 1931.
10. ———: The Glossy Petal of *Ranunculus*: a correction. Ann. Bot., xlvi, 188–90, 1932.
11. ———: The Structure of the Starch Layer in the Glossy Petal of *Ranunculus*. II. The British Species Examined. Ibid., xlix, 283–9, 1935.
12. Smith, G. H.: Vascular Anatomy of Ranalian Flowers. I. Ranunculaceae. Bot. Gaz. lxxxii, 1–29, 1926.
13. Thompson, J. M.: Comments on Recent Statements regarding the Nature and Origin of the Angiospermic Stigma. New Phyt., xxxiii, 306–15, 1934.
14. Troll, W.: Organisation und Gestalt im Bereich der Blüte. Berlin, 1928.
15. Worsdell, W. C.: The Principles of Plant-Teratology, i. London, 1915.

Curtis's Bot Mag Tab 9380 *R. asiaticus* L. var albiflorus. Single form [T. 370. b. 3.135]
Baker a Cretan form. Journ Roy Hort Soc 54. 395. 1929
Various ? clone forms have been found wild.
Le Journ Genetics 26. 257 P. 380. b. 21. 23-25

ARBER, AGNES

STUDIES IN FLOWER STRUCTURE

III. ON THE 'CORONA' AND ANDROECIUM IN CERTAIN AMARYLLIDACEAE

Reprinted from Annals of Botany
New Series Vol. I No. 2 April 1937
Pages 293–304

Printed in Great Britain

from serial sections through a bud. B1 shows the structure at the level at which the stamen-cup is just becoming free from the perianth segments. In

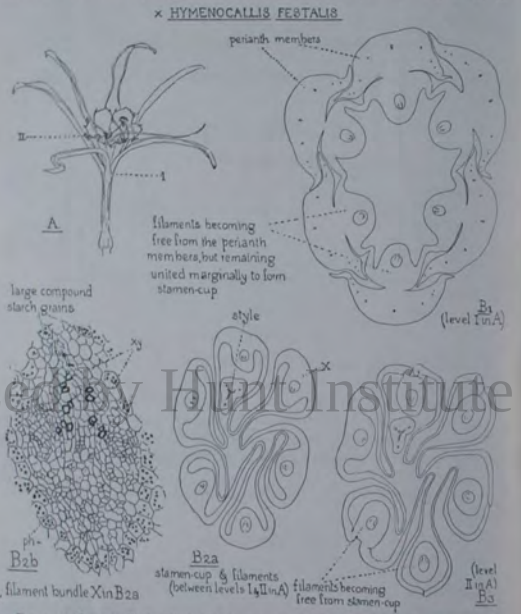

FIG. 1. ×*Hymenocallis festalis*, hybrid between *H. calathina* Nich. and *Elisena longipetala* Lindl. (Major Pam, May 2, 1935). A, flower (×⅓ *circa*). B1–B3, sections from a transverse series passing upwards from below through a bud. B1, B2*a*, B3 (×9 *circa*). B1, at level I in A, gynaeceum omitted. B2*a* and B3, sections through stamen-cup and style, perianth omitted. B3, at level II in A. B2*b*, filament X in B2*a* (×99 *circa*); starch grains are not shown in any other figure. Throughout the figures in this paper, *xy* = xylem, and *ph* = phloem.

B2*a* it is completely detached, while in B3 it is cut just below its upper margin, where the filaments are becoming free; in these two figures the perianth is not shown. The filaments are massive, and each has a single large bundle.

One of these is shown in B2*b*; there are indications of radial arrangement of the elements, suggesting that some secondary development has taken place. The part of the stamen-cup between the filaments is entirely non-vascular.

Hymenocallis amancaes Nich. and *Pancratium illyricum* L. I have cut serial sections of a flower of each of these two species, grown by Major Pam. I find that the 'coronal' structure shows no essential difference from that described for *H. festalis*.

Eurycles Cunninghamii Ait. This species was introduced from North Queensland by Lady Rockley. The stamen-cup, which is shown laid open in Fig. 2, D, p. 296, is lobed and bifid between the filaments. Sections such as that drawn in Fig. 2, F, show that, in the origin of the stamen-cup and its relation to the perianth, this species closely resembles *Hymenocallis festalis*. A detail that may be mentioned, though it does not bear upon our present inquiry, is that the anther at its base completely enrings the filament (E), a condition which I have also noticed in one of the Gramineae, *Anomochloa marantoidea* Brongn. (Arber, 1929) and in one of the Capparidaceae, *Gynandropsis speciosa* DC.

Eustephia pamiana Stapf. This Argentine species (Stapf, 1929), of which I have examined material grown by Mr. Bowles, is included here because, although it has no stamen-cup, its free filaments are winged (Fig. 2, A, p. 296). B1 is a section through the flower at a level corresponding to the sections of other genera shown in Fig. 1, B1, p. 294, and Fig. 2, F.

(b) *Coronatae*.

In this tribe I have been able to examine only species belonging to the genus Narcissus.

Narcissus ? minor. Serial sections were cut through a bud of a garden form grown under this name. Fig. 3, A1, p. 297, passes through the perianth tube, which in A2 is beginning to separate into corona and perianth segments. Owing to a slight obliquity in the section, the level just below the separation is shown on the left-hand side, and it is seen that while still in the perianth tube, the bundles have divided to form two series, the outer destined for the perianth segments and the inner for the corona. The bud was so young that lignification was only just beginning in the corona and perianth segments, but here and there, in bundles which happen to be more advanced than the rest, it is seen that the coronal strands are not orientated normally, but have their xylem directed towards the xylem of the perianth bundles; in other words, the coronal bundles have dorsal xylem and ventral phloem, while the perianth bundles have, as usual, ventral xylem and dorsal phloem. This distinction is seen in Fig. 3, B. In Fig. 4, C1–C5, p. 299, from a series passing upwards from below, the origin of the two opposed bundles, *m'* and *m''* in Fig. 3, A1, p. 297, can be traced. The normally orientated strand (C1) widens (C2), and divides into two bundles, *m* and *n*, facing one another in a plane parallel to the surface of the perianth tube (C3). One of these, *m*,

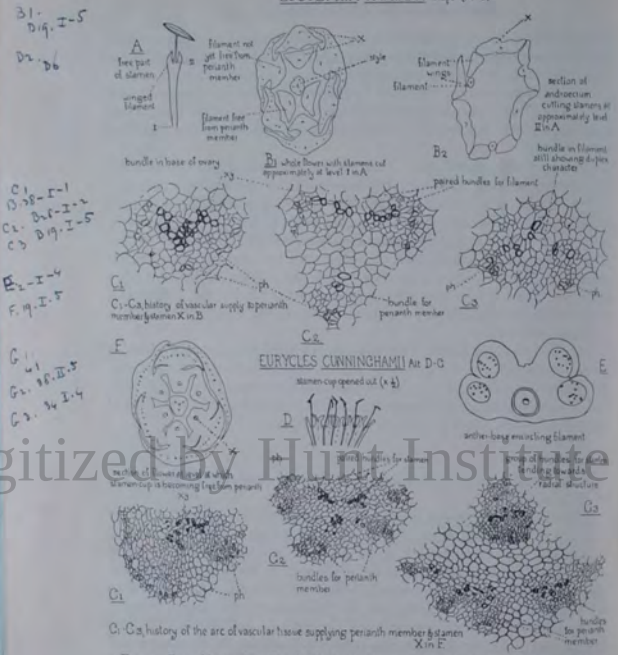

FIG. 2. *Eustephia pamiana* Stapf (Mr. E. A. Bowles, April 22, 1936). A, free part of one stamen (nat. size, *circa*). B1 and B2, sections from series through a young flower (×14); B1, cutting stamens at approximately the level of I in A; B2, showing androecium only, approximately at level II in A. C1–C3, sections (×193 *circa*) from a series from below upwards, to show the history of the bundle supplying stamen and perianth member X in B1. These diagrams are orientated differently from B1, so as to bring the adaxial faces uppermost. C1, in base of ovary; C2, in top of ovary; C3, in free part of filament just above level of B1. D–G, *Eurycles Cunninghamii* Ait., from a plant exhibited at the Roy. Hort. Soc. by Lady Rockley, June 5, 1935. D, stamen-cup opened out (×½); E, transverse section of a stamen near the base of the anther (×23); F, transverse section through flower at level at which the stamen-cup is being detached from the perianth members (×7). G1–G3, sections (×77) from a series from below upwards to show the history of the vascular supply for stamen and perianth member X in F. G1, from a section at base of gynaeceum below ovary cavities, to show arc of vascular tissue shortly above its emergence from the vascular ring of the pedicel; G2, at a higher level in the ovary wall; G3, in the perianth tube.

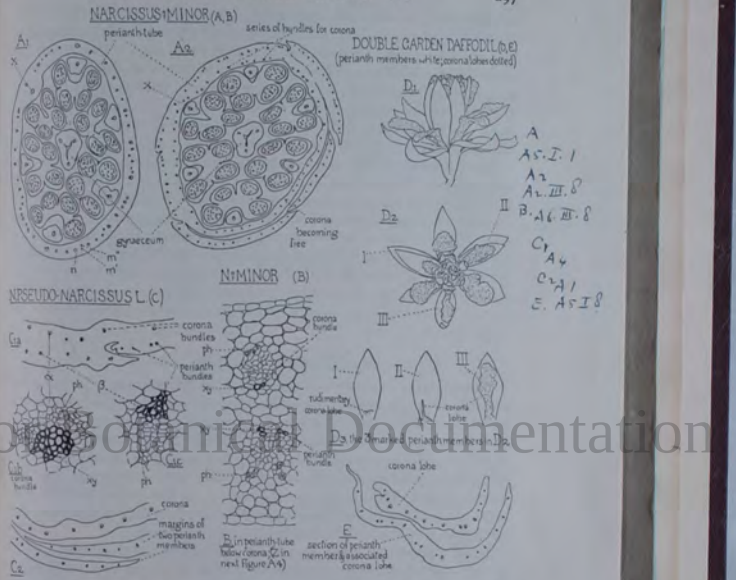

FIG. 3. A, B, *Narcissus ? minor*. A1 and A2, transverse sections through the perianth tube of a bud below and just at the level of the detachment of the corona (×14). The origin of the perianth and stamen bundle X is shown in Fig. 4, A1–A5, p. 299, and of *n*, *m'*, and *m''*, in Fig. 4, C1–C5. B, the two bundles in the perianth tube marked z in Fig. 4, A4 (×193 *circa*). C, *N. pseudo-narcissus* L. (wild form). C1*a*, segment of top of perianth tube showing two series of bundles, one of which is normally orientated for perianth, while the other is inverted for corona (×14). Two of these bundles, *α*, corona bundle, and *β*, perianth bundle, are drawn (×193 *circa*) in C1*b* and C1*c*. C2 (×14) at a level above C1*a*, to show the separation of the perianth segments and corona, which are still united in C1*a*. D, double daffodil (garden form); D1–D3 (×½); perianth white, corona lobes, dotted. D1 and D2, flower from the side and above. D3, the three outer perianth segments with their associated corona lobes (×½). E, transverse section of a perianth segment and associated corona lobe (×14).

divides into two, *m'* and *m''*, in this plane (C4), and the phloems move round until the bundles face one another (C5).

Narcissus pseudo-narcissus L. Since the bud of *N. ? minor* described above

was too young to show full lignification, I have added sections through the flower of a wild daffodil, in which the bundles were completely developed, so that the orientation of the coronal strands is clear. Fig. 3, C1*a*, shows the structure of a small part of the upper region of the perianth tube; the overlapping margins of two perianth segments are seen just becoming free from the tube. In C1*b* and C1*c*, a coronal bundle, α, and a perianth bundle, β, are drawn on a larger scale. It will be noticed that the inverted coronal bundle has more massive xylem than the perianth bundle.

The behaviour of the corona in double forms of *N. pseudo-narcissus* is of some interest. There is much variation in structure among these flowers, but in characteristic examples there is generally no 'trumpet', and each of the numerous perianth segments bears on its inner face a separate lobe, exactly resembling the corona of the normal form in colour and texture (Fig. 3, D1–D3). Serial sections through these perianth segments, with their associated lobes (Fig. 3, E), reveal the normal orientation of the bundles in the perianth segments, but, in the corona lobes, the reversed position and stronger lignification which have been already noticed in the corresponding parts of the single flower.

(ii) *The interpretation of the 'corona'*

It would serve little purpose to enter in detail into the history of the earliest opinions about the corona; but as examples of views that have been held, it may be mentioned that the corona of Narcissus was described by Doell in 1857 as comparable with the ligules of certain foliage leaves, by Masters in 1865 as consisting of modified stamens, and by Smith in 1866 as composed of confluent petal stipules. Most of the earlier writers dealt with Narcissus only; and those who brought any member of the Pancratieae into the argument seem always to have assumed that the staminal cup of this tribe must be explained on the same lines as the corona of Narcissus.

In 1875 Eichler reviewed the subject and came to the conclusion that the corona was not staminal, but was an outgrowth of the perianth, both in Narcissus (Coronatae) and in members of the Pancratieae. On the other hand, in 1888 Pax interpreted the corona of the Pancratieae as staminal stipules, and regarded that of the Coronatae as a corresponding structure, which had, however, become ligular and free from the filaments. Ten years later Čelakovský (1898) concluded, like his predecessors, that the corona in the Pancratieae and in the Coronatae is of the same nature.

Coming to the present century, we find that Velenovský in 1910 supported the view that the corona was always of the nature of fused staminal stipules, while, as lately as 1933, the same conclusion is maintained in the most recent edition of Goebel's 'Organographie', in which a hypothetical diagram is given (Fig. 1951, p. 1865) tracing the assumed development of the free corona of Narcissus from the stamen-cup of the Pancratieae.

It is remarkable that the numerous botanists who have approached the

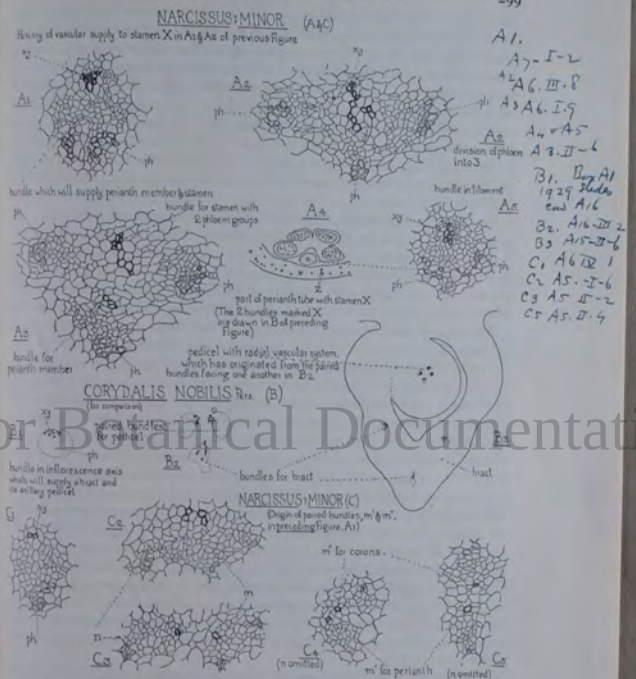

FIG. 4. A and C, *Narcissus ? minor*. A1–A5, from a series of sections from below upwards, tracing the history of the vascular supply to stamen X in Fig. 3, A1, A2. A1–A3, A5 (×193 *circa*); A4 (×14). B, *Corydalis nobilis* Pers. B1–B3, transverse sections (×47) from a series from below upwards through an inflorescence axis showing the origin of the vascular system for a bract and pedicel; xylem elements alone indicated. (A bundle supplying the keel of the bract, which is merely a branch of the median bundle, is not represented.) C, *Narcissus ? minor*. C1–C5, sections from a series from below upwards (×193 *circa*) through the perianth tube below Fig. 3, A1, p. 297, to show origin of bundles *n*, *m'*, and *m''*; in C4 and C5, *n* is omitted.

MASTERS, M. T., 1865. On the Corona of *Narcissus*. Seemann's Journ. Bot., iii. 105–9.
PAX, F., 1888: Amaryllidaceae, in Die natürlichen Pflanzenfamilien, Engler, A. and Prantl, K., ii. 5. 97–124.
SMITH, W. G., 1866: The Corona of *Narcissus*. Seemann's Journ. Bot., iv. 169–71.
STAFF, O., 1929: *Eustephia pamiana*. Curtis's Bot. Mag., (1929 for 1927) cliii. pt. I, tab. 9164.
TIEGHEM, P. VAN, 1871: Recherches sur la structure du pistil et sur l'anatomie comparée de la fleur. Mém. prés. par div. sav. à l'Instit. de France, xxi. 1–261.
VELENOVSKÝ, J., 1907: Vergleichende Morphologie der Pflanzen. II. Prague.
—— 1910: Vergleichende Morphologie der Pflanzen. III. Prague.
WORSDELL, W. C., 1915: The Principles of Plant-Teratology. I. Ray Society, London.

12

THE INTERPRETATION OF THE FLOWER: 13 A STUDY OF SOME ASPECTS OF MORPHOLOGICAL THOUGHT

BY

AGNES ARBER

[REPRINTED FROM BIOLOGICAL REVIEWS, VOL. 12, 1937, p. 157]

CAMBRIDGE: AT THE UNIVERSITY PRESS

PRINTED IN GREAT BRITAIN

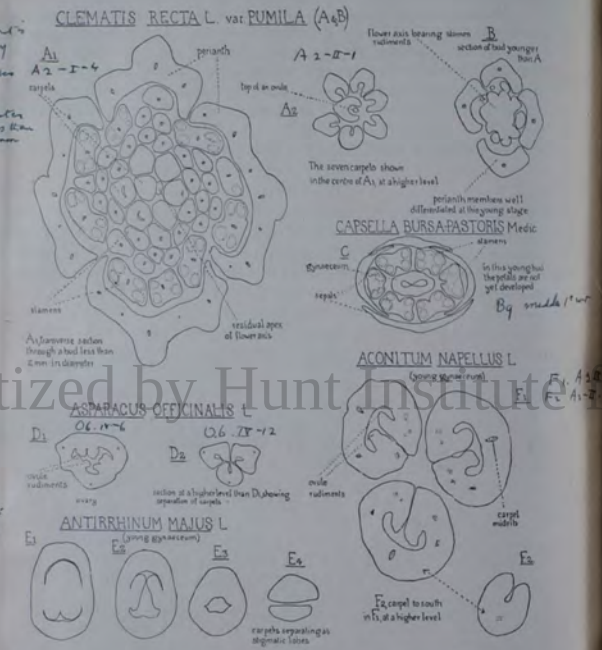

Fig. 2. All the diagrams from transverse microtome series from below upwards through young buds. A, B, *Clematis recta* L. var. *pumila* (Cambridge Bot. Gard.). Sections (×47). A_1, young bud; A_2, gynaeceum only of the same bud at a higher level. B, younger bud. C, *Capsella Bursa-pastoris* Medic., young bud (×77 *circa*). D, *Asparagus officinalis* L. D_1 and D_2, very young gynaeceum (×47). E, *Antirrhinum majus* L., four sections from series through a young gynaeceum (×47). F, *Aconitum Napellus* L. F_1, very young gynaeceum cut in ovary region; F_2, "south" carpel in F_1 at a higher level.

has been made by Goebel (1933, p. 1821). He describes the gynaeceum as formed of megasporophylls (carpels), bearing ovules on their margins, which are incurved and fused with one another, or with those of other megasporophylls. Considering the range of variation among angiospermous gynaecea, it was a bold measure on the part of the early morphologists to seek to bring them all under this simple and uniform conception—but the event has proved that it "works". Systematists have found it possible to use it for the description and comparison of the female organ in the plants with which they deal; Engler (1926), for instance, after more than fifty years of taxonomic work, stated definitely that he adopted the foliar carpel view for all angiosperms. The validity of the theory has, however, been disputed in recent years, and it seems necessary to present some of the evidence for it, since—as one of its opponents has pointed out—"Aucun ouvrage ne contient un exposé complet et ordonné des arguments que l'on a produits en faveur de cette interprétation" (Grégoire, 1931). An exhaustive review of the arguments for and against this theory would involve a detailed account of the structure of every type of gynaeceum in the angiosperms. This is an impracticable task, but as a small step in this direction, I have made an examination of serial sections of flowers belonging to a number of both dicotyledons and monocotyledons—some of them chosen as test cases. The result has been to fill me with wonder at the insight shown by the earlier morphologists in envisaging the carpel and foliage leaf as members of the same category, when they had to study them without the advantages of modern technique. Some of the sketches in Fig. 2 show how microtome sections of young gynaecea may serve to illustrate the Candollean theory. In Fig. 2, F_1, the three follicles of *Aconitum Napellus* L. are drawn at a very young stage, and it will be seen that the carpellary margins bearing the rudimentary ovules are free from one another, though appressed. Freedom of carpellary margins in young monocarpellary gynaecea has been figured by McLean Thompson (1929) for a number of legumes, and by Joshi (1934, Fig. 1, 6, p. 969) for *Boerhaavia*, while it is shown here (Fig. 3, *4 a, b*) for *Mirabilis*. Fig. 2, D_1, is from a transverse series through a young gynaeceum of *Asparagus officinalis* L., in which the three carpels, instead of being free like those of *Aconitum Napellus*, are united by their ovule-bearing margins. At a higher level, however, they separate (D_2), and their upper regions show the same leaf-like character as those of *Aconitum* (F_2) and *Clematis* (A_2). The similarity of the young carpel of *Ranunculus* to a leaf rudiment has been noted by Salisbury (1931, pp. 558–9). In the gynaeceum of *Antirrhinum majus* L., in which each of the two carpels has its margins united, and also fused with those of the other carpel, serial sections passing upwards to the stigmatic region show that the margins of each carpel come apart near the top of the ovary (E_2), and that, above this, the two carpels separate (E_4). Moreover, it is not only shape which is explicable on the Candollean hypothesis; internal structure, also, often follows just the lines which, on this hypothesis, might have been predicted. As an example we may take the anatomy at the base of the gynaeceum in *Hypericum hirsutum* L., which is illustrated in Fig. 4, A_1–A_3. Here, after the bundles for the stamen phalanges have been given off, three arcs of vascular tissue are left for the

division is seen quite simply as *separation* of the united bundles belonging to the fused margins of adjacent carpels.

On general grounds, a serious argument against Dickson's theory is that it is an *ad hoc* hypothesis, which cannot be applied consistently even throughout the Papaveroideae. It involves explaining most of the genera in this tribe on the "sterile" and "fertile" carpel hypothesis, while retaining the classic hypothesis for *Platystigma*, *Platystemon*, and *Romneya*. The gynaecea of these three genera do not seem, however, to differ fundamentally in structure from those of the rest of the tribe; and one cannot but distrust a theory which offers a basically different explanation for the well developed fused marginal veins of *Romneya*, and for the placental veins of *Glaucium*, in which the same rich development of the marginal carpellary regions occurs, although in a more highly elaborated form.

VII. STIGMA AND TRANSMITTING TISSUE

In certain recent interpretations of the gynaeceum, there has been a tendency to treat the "stigma" as if it were a definite morphological entity. This tendency has been criticized by more than one writer (see especially Bremekamp, 1934, p. 2, footnote). As a matter of fact, the surfaces which receive the pollen merely mark the upward terminations of the tracts of tissue along which the pollen tube makes its way to the ovule; and the position of these "stigmatic" surfaces, in relation to the gynaeceum as a whole, shows a good deal of variation. Hamshaw Thomas (1934) has emphasized the incompleteness of our knowledge of what was formerly called the "conducting tissue". This, and "stylar core" which I previously used (Arber, 1934), are unsatisfactory terms for the path of the pollen tube, and the name "transmitting tissue" (suggested by T. M. Harris and adopted by Hamshaw Thomas) is certainly better; it might be well, in addition, to use "transmitting tract" for regions in which the tissue in question is merely a surface feature.

Our information about transmitting tissue goes back to Capus (1878) and Guéguen (1900–2), who showed that conduction of the pollen tube is, as a rule, effected by the inner faces of the two carpellary margins, and of the placentae which are emergences from these margins; the transmitting tissue for each carpel is thus double in origin (cf. Fig. 3, *4*). The tissue involved is the epidermis, reinforced by underlying elements. A different view has been suggested by Joshi's recent work (1934). He describes the transmitting tissue (for which he uses the term "stylar canal") in various plants, and states that "the stylar canals are either continuous with the ventral traces of the carpel or make their appearance at, and occupy exactly the situation of, such traces. The conclusion is reached that the stylar canals have been derived from, and represent modified ventral bundles of, the carpels." This conclusion, if it could be substantiated, would be a very remarkable one, because a stylar canal could not perform its function unless it connected with the ovary cavity—a thing which it could scarcely do if it represented the continuation of one of the ovary bundles. In order to test Joshi's theory, I have cut serial sections of gynaecea of *Mirabilis Jalapa* L., one of the species which he describes. This plant

was also dealt with formerly by Guéguen, who stated that the transmitting tissue descends vertically in the posterior wall of the ovary and expands at the bottom of the cavity into an annular mass which surrounds the funicle. My observations confirm this description (Fig. 3); they are not in accordance with Joshi's statement

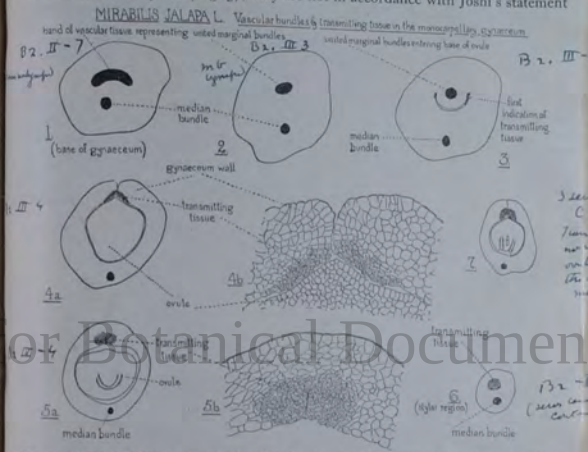

Fig. 3. *Mirabilis Jalapa* L. (Cambridge Bot. Gard.). 1–6, transverse sections from microtome series from below upwards through a bud at the stage at which the style had not elongated, but the pollen-grains were already mature (at this stage carpel still open). 1, 2, 3, 4 *a*, 5 *a*, 6 (×47); 4 *b* and 5 *b* (×193 *circa*). 7, transverse section from a carpel of another flower to show topography of ovule, which is not seen in the series 1–6 (×47). Vascular bundles indicated in solid black, transmitting tissue cross-hatched in the low power, and dotted in the high power diagrams; this dotting is merely a conventional symbol to indicate the relatively rich, deeply staining cell contents of the transmitting tissue.

that "the stylar canal occupies the place of the ventral traces of the carpel". I find that the transmitting tissue is formed as usual from epidermal and subepidermal layers, and that it appears to bear no relation to the fused ventral bundles which enter the base of the ovule (Fig. 3, *3*).

There is little doubt that the description of the transmitting tissue of angiosperms given by Capus and Guéguen is, in a general way, correct in outline, though their work, having been done merely with the aid of hand sections, needs supplementing with more exhaustive microtome work. I include figures here illustrating the course of the transmitting tissue in the syncarpous gynaeceum of *Hypericum*, for comparison with the monocarpellary gynaeceum of *Mirabilis*. In Fig. 4, A_4,

the three ovule-bearing placentae almost meet in the centre of the ovary; their inner surfaces are clothed with a secretory epidermis which forms the transmitting

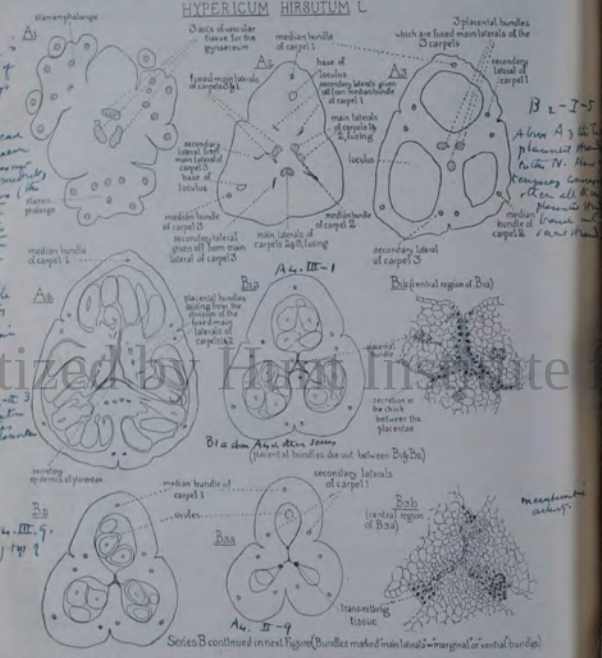

Fig. 4. *Hypericum hirsutum* L. (Wharfedale). Sections from transverse series from below upwards; A_1–A_4, through the lower part of one gynaeceum, and B_1–B_5, through the upper part of another. B_1 *b* and B_2 *b* (× 193 *circa*); all the other figures × 47. The elements of the epidermis, which forms the transmitting tract for the pollen tubes, are indicated individually in A_1, B_{1a}, and B_2.

tract. In B_1 *a*, another gynaeceum is shown cut at a higher level, above the insertion of the ovules. Its central region is drawn in B_1 *b*; the epidermis with its rich contents, and the secretion which exudes from it into the crannies, are indicated.

It will be seen from B_1 *a* and B_1 *b* (see also Fig. 5, C_2) that the transmitting tract extends down to a level below the tops of the placental (ventral) bundles, and that it does not replace these bundles in position, as it should on Joshi's theory. In B_3 *a*, *b*, the three-armed chink between the placentae has partially closed, and, at the junction between each arm and the loculus, the elements of the secretory epidermis

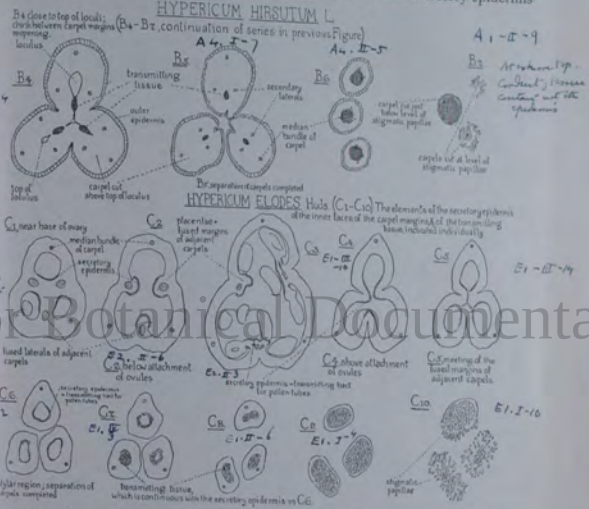

Fig. 5. B_4–B_7, *Hypericum hirsutum* L., continuation of series in Fig. 4, from top of loculi to stigmatic region (× 47). Elements of outer epidermis indicated individually; transmitting tissue cross-hatched. C_1–C_{10}, *Hypericum Elodes* Huds., sections from a transverse series from below upwards through a gynaeceum. C_1, near base of ovary below attachment of ovules; C_{10}, stigmas. All × 47. Elements of the transmitting tract (secretory epidermis), and of the transmitting tissue into which it passes, indicated individually.

are multiplying to form the transmitting tissue. The process can be followed further in Fig. 5, B_4, in which, owing to a slight obliquity in the section, three stages in the disappearance of the loculus and the development of the transmitting tissue can be seen. In B_5, the styles have separated, and the transmitting tissue appears as an isolated patch embedded in the mesophyll of each carpel, but the preceding sections make it clear that it is in reality a continuation of the superficial tissue of the inner carpellary margins; it is in fact the only relic at this level of the inner (upper)

in focus is needed before we can hope for clear illumination upon such problems as the origin of the flower.

Another attempt at a phylogenetic interpretation of floral morphology is that of Zimmermann (1930). The lines upon which this attempt is made differ markedly from those followed by Arber & Parkin, or by Hamshaw Thomas, since Zimmermann chooses a very much earlier starting point. He bases his whole interpretation on the idea that the type of structure shown by the Devonian Rhyniaceae is primordial for the Cormophytes. This procedure is open to the fundamental objection that we are by no means certain that *Rhynia* was a primitive type. As Goebel wrote (1933): "Möglich, dass sie eine sehr primitive, möglich auch, dass sie eine stark abgeleitete war!" If, however, we put this objection on one side, and follow Zimmermann's argument as he passes the vegetable kingdom in review, we find that *Rhynia* certainly serves to some extent as a useful term of comparison so long as he is dealing with the vascular cryptogams, but that when the higher plants are reached the clue seems to be lost. The part of the book dealing with the angiosperms is relatively confused and incoherent—an inevitable result of the attempt to fit the facts of floral structure into a scheme based upon the organization of a group with which it may well be that the forbears of the angiosperms never had any connexion.

XI. THE REACTION FROM PHYLOGENETICS

In recent years there has been a marked reaction among students of the flower against the identification of morphology with phylogenetics. Zimmermann (1930, 1934), recognizing the inherent difficulties in the way of race phylogeny ("Sippenphylogenie"), makes an interesting effort to replace it to some extent by "Merkmalsphylogenie", i.e. the phylogeny of single characters; but this, when analysed, seems to be little more than a version of idealistic morphology, with the attempted addition of a time element. The table (1930, pp. 334–7) in which he arranges numerous floral and vegetative characters of the angiosperms as "primitive" or "derived", shows that, though "Merkmalsphylogenie" claims to be independent of "Sippenphylogenie", it continually slips back into it.

The reaction against phylogeny is merely foreshadowed in Zimmermann; but it is fully developed in the work of McLean Thompson (1934*a* and other papers of this series; 1934*b*, 1935; for critical discussion see Clapham, 1934 and Bancroft, 1935, pp. 90–4). McLean Thompson's standpoint is so remote from that of phylogenetics as to lead him to the conclusion that "the real problem of floral morphology is that of the physiology of growth of a sporogenous axis". At present, however, we are so far from a synthesis of morphology and physiology that morphological problems cannot be restated in terms of physiology, except by a process of abstraction which omits essential elements. For this reason I think that, despite the interest of the ontogenetic data which he provides, McLean Thompson's *theories* hardly come within the province of a morphological discussion. From the point of view of theoretical morphology, the great value of his contribution seems to me to lie in his emphasis on holism, as in his dictum—"the mystery of the carpel is that of the flower as a whole".

For comparison of simple carpel flowers: Nehemiad Grew
see my Artistotle Grew, p. 62

XII. "GESTALT" MORPHOLOGY

Another recent writer who discards the phylogenetic aim—Wilhelm Troll—differs fundamentally from McLean Thompson, since he contends that morphology can never pass over into physiology. He returns to the standpoint of Goethe in holding that morphology *is* comparative morphology. He considers that the subject was developing in a more hopeful direction in the period before it was diverted by Darwin's influence into the service of evolutionary speculation—a view which had already been suggested elsewhere (Arber, 1925). It will be worth while here briefly to indicate the scope of Troll's book on the flower (1928), since little attention has been paid to his ideas in this country, despite an interesting review by Rendle (1929). This neglect is not unnatural, since Troll's notions do not lend themselves to concise expression, and it takes time to disengage them from the somewhat confusing background upon which he presents them.

Troll considers that, according to the point of view from which the flower is regarded, it may be treated as (i) a biological type, (ii) an organization type, or (iii) a "Gestalt" type. When regarded as a *biological type*, the flower is seen ecologically, in relation to insect visitors and other environmental factors. When regarded as an *organization type*, it is understood in a sense which would ordinarily be called morphological; that is to say, it is treated structurally, as formed of units such as petals, carpels, etc., arranged according to a definite architectural scheme. The flower as seen from these two familiar standpoints is not, however, the subject with which Troll is concerned; his book deals with the flower from the third standpoint, as a "*Gestalt*" *type*. In trying to convey the gist of his "Gestaltlehre", one is faced by the serious difficulty that his views involve a reorientation of the orthodox outlook, and that the English language and mode of thought are ill adapted for expressing the sort of idea to which he desires to give currency. A large part of the book is devoted to an extremely detailed analysis of various resemblances which have no phylogenetic basis, such as those between pseudanthia (inflorescences simulating flowers) and euanthia (simple flowers). Most botanists dismiss resemblances of this kind as empty curiosities which are scarcely worth thinking about, or else label them as "adaptations", but Troll finds in them the text for a new morphology. His intensive study of these resemblances—which have long been recognized in outline—gives a cumulative impression, to which it is impossible to do justice in a brief summary. I will now only attempt to make his meaning emerge from a few examples; his own descriptions and figures must be consulted before his conclusions can be evaluated fairly.

The similarity of the involucre to a calyx, and of the ray florets to a corolla is especially noticeable in some composites in which the number of bracts and ray florets is small. *Chrysogonum virginianum* L., for instance, has an involucre consisting of five bracts in one whorl, recalling a calyx, and five ray florets suggesting petals—the whole producing a strikingly flower-like effect. As Troll's emphasis is on form rather than on organization, he is led to pay special heed to petals, since they are primarily responsible for the form of flowers; this is a contrast to the usual

McCLURE, F. A. (1934). "The inflorescence in *Schizostachyum* Nees." *J. Wash. Acad. Sci.* **24**, 541–8.
MARSDEN-JONES, E. M. (1935). "*Ranunculus Ficaria* Linn.: life-history and pollination." *J. linn. Soc. (Bot.)*, **50**, 39–55.
NÄGELI, C. VON (1884). *Mechanisch-physiologische Theorie der Abstammungslehre*. Munich and Leipsic.
NEWMAN, I. V. (1936). "Ontogeny of the angiospermic carpel." *Nature*, Lond., **137**, 70–1.
RENDLE, A. B. (1929). Review of Troll, W. (1928) in *J. Bot.*, Lond., **67**, 341.
SAHNI, B. (1935). "Homoxylon and related woods and the origin of angiosperms." *Proc. Sixth Intern. Bot. Congress, Amsterdam*, **2**, 237–8.
SALISBURY, E. J. (1931). "On the morphology and ecology of *Ranunculus parviflorus*, L." *Ann. Bot.*, Lond., **45**, 539–78.
STACE, W. T. (1920). *A Critical History of Greek Philosophy*. London.
THOMAS, H. HAMSHAW (1925). "The Caytoniales, a new group of angiospermous plants from the Jurassic Rocks of Yorkshire." *Philos. Trans.* B, **213**, 299–363.
—— (1931). "The early evolution of the angiosperms." *Ann. Bot.*, Lond., **44**, 647–72.
—— (1932). "The old morphology and the new." *Proc. Linn. Soc. Lond.* **145** (1932–3), 17–32.
—— (1934). "The nature and origin of the stigma: a contribution towards a new morphological interpretation of the angiosperm flower." *New Phytol.* **33**, 173–98.
—— (1935). "Floral morphology in the light of palaeobotanical knowledge." *Proc. Sixth Intern. Bot. Congress, Amsterdam*, **2**, 122. "Pteridosperm Evolution and the Angiospermae." *Ibid.* p. 230.
THOMPSON, J. MCLEAN (1924). "Studies in advancing sterility. Part I. The Amherstieae." *Publ. Hartley bot. Lab. Lpool. Univ.* **1**, 1–54.
—— (1929). "Studies in advancing sterility. Part IV. The legume." *Publ. Hartley bot. Lab. Lpool. Univ.* **6**, 1–47.
—— (1934*a*). "Studies in advancing sterility. Part VII. The state of flowering known as angiospermy." *Publ. Hartley bot. Lab. Lpool. Univ.* **12**, 1–47.
—— (1934*b*). "Comments on recent statements regarding the nature and origin of the angiospermic stigma." *New Phytol.* **33**, 306–15.
—— (1935). "The acarpous nature of modern flowering." *Proc. Sixth Intern. Bot. Congress, Amsterdam*, **2**, 122–4.
THEGHEM, P. VAN (1871). "Recherches sur la structure du Pistil et sur l'Anatomie comparée de la Fleur." *Mém. Acad. Sci.*, Paris, **21** (1875), 1–261.
TROLL, W. (1928). *Organisation und Gestalt im Bereich der Blüte* (*Monogr. zeitr. Bot.* **1**), Berlin.
VIDAL, L. (1908). "Recherches sur le sommet de l'axe dans la fleur des Gamopétales." *Thèses prés. à la Fac. des Sci. de Paris pour le grade de docteur ès sc. nat.* sér. A, 360, **1025**, 1–115.
WIELAND, G. R. (1906). *American Fossil Cycads*, **1**. Carnegie Institution, Washington.
ZIMMERMANN, W. (1930). *Die Phylogenie der Pflanzen*. Jena.
—— (1934). "Research on Phylogeny of Species and of Single Characters (Sippenphylogenetik und Merkmalsphylogenetik)." *Amer. Nat.* **68**, 381–4.

ADDENDUM. 23 *November* 1936

Since the present review was in print, the memoir to which Newman, I. V. (1936) forms the preliminary note, has appeared in *Proc. Linn. Soc. N.S.W.* **61**, 56–88. The conclusion is reached (p. 75) that the legume in the two species of *Acacia* examined "is a lateral laminar organ developed on an apex which is immediately suppressed; that the initiation and differentiation of the legume is not significantly different from those of a vegetative leaf; and that the ovules are formed on the margins of the lamina of the legume".

I have spoken in Section II of the nature of the free-central placenta in the Primulaceae as still a matter of controversy, but the subject has since been put upon a different plane by Dickson, J. (1936), "Studies in floral anatomy III. An interpretation of the gynaeceum in the Primulaceae", *Amer. J. Bot.* **23**, 385–93. Dickson's work fully establishes her conclusion that "the 'free-central placenta' of the Primulaceae may be interpreted as the fused margins of five carpels (± residual axial tissue)".

A summary of Foster's work, to which reference is made in Section VIII, has now appeared (1936), "Leaf differentiation in angiosperms", *Bot. Rev.* **2**, 349–72.

The following titles should be added to the references:

Grégoire, V. (1935). "Sporophylles et organes floraux, tige et axe floral." *Rec. Trav. bot. néerland.* **32**, 453–66.
Joshi, A. C. (1935). "Criticism of Dr Thomas's recent hypothesis on the nature of the angiospermous carpel", with a reply by Dr Hamshaw Thomas. *J. Bot.*, Lond., **73**, 286–94.

ARBER, AGNES

STUDIES IN FLOWER STRUCTURE

IV. ON THE GYNAECEUM OF PAPAVER AND RELATED GENERA

Reprinted from Annals of Botany
New Series Vol. II No. 7 July 1938

Printed in Great Britain

(De Candolle. Organographie végétale II 40 fr de Candolle's very odd term, the receptacle, the Papaver capsule forms an extra skin pouring up the gynaecium)

Studies in Flower Structure

IV. On the Gynaeceum of Papaver and Related Genera[1]

BY

AGNES ARBER

With seven Figures in the Text

I. Introduction

THE morphological interpretation of the gynaeceum in the Papaveraceae has been a matter for discussion since the time of A. P. de Candolle (1827), and widely varying opinions on the subject have been expressed by botanists of the present day. In the hope of obtaining further evidence bearing on the subject I began, some years ago, to cut serial sections of the flowers of members of this family; and, after examining a number of genera, I came to the conclusion that a special study of the genus Papaver might be a useful contribution. This genus was chosen partly because it affords a good test case, and partly because—although it is so familiar an object—our knowledge of its construction is still imperfect. Lignier's pioneer work (1911, 1915) on the anatomy of the gynaeceum in the Papaveraceae, which was left unfinished at his death, did not include Papaver, and later writers who have considered the genus have given accounts which are incomplete in certain critical directions.

In the following pages my observations on Papaver and related genera will be described, and their theoretical bearing will then be discussed. The terminology used in the descriptions and figures will be based, provisionally, upon the hypothesis that the carpels form one whorl of similar members, and that the placentae are joint outgrowths from their united margins. This is the theory which, on the evidence of external features, has been adopted generally by systematists, but it has never been tested by detailed application to the minuter structure of the gynaeceum of Papaver. When this gynaeceum

[1] This paper represents part of the work carried out during the tenure of a Leverhulme Research Fellowship. The writer is indebted for material to the Director of the Cambridge Botanic Garden.

has been described in full on this basis, we shall be in a position to determine whether, from the point of view of structural evidence, the theory is self-consistent, and also whether it enables us to relate the gynaeceum of Papaver to that of other members of the family.

II. Observations

It is convenient to begin the study of Papaver with a species which has relatively few carpels, and, for this reason, *P. Argemone* L. may be used as a type. The fruit is seen in Fig. 1, A, while B1–B6 represent transverse sections from a series through a very young gynaeceum. In each of these sections one of the carpels is, for clearness, delimited by arrows. B1, cut at the extreme base, shows the four carpels surrounding a minute central area of tissue, differing from them histologically; this is the vestigial apex of the floral axis. Each carpel at this level has its placental outgrowths appressed to enclose a loculus. The median strands of the carpels are scarcely distinguishable. There is no lignification except in the bundles on the radii of the placentae; these strands are interpreted as the united marginals of adjacent carpels. B2 is cut above the tip of the floral axis. The sterile basal regions of the four placentae now project freely into the cavity, and the median bundles of the carpels are becoming better defined than at lower levels. In B3 we pass to the ovule-bearing region of the ovary. The gynaecium is so young that the ovules are still atropous, though the rudiments of the integuments are already visible. This diagram may be compared with Fig. 2, C1, which represents the fertile region of an older gynaeceum of the six-carpelled type. In Fig. 1, B4, we reach the level of the upper sterile region of the ovary, where it is passing into the stigmatic crown. We see here the reappearance of the individual loculi (cf. also Fig. 2, C3*a*), which were defined at the base of the ovary (B1), but which, between these levels, were merged in the general cavity. In B5, which is still higher, not only the loculi, but also the median regions of the carpels, are dying out, and they have disappeared before B6 is reached. In B4 and B5, as well as in Fig. 2, C3*a* and C4*a*, the centre of the section is occupied by a transmitting canal lined with papillae. In B4 the transmitting canal has four rays—the slits between the appressed placentae. In B5, and in Fig. 2, C3*a*, a second set of rays has developed, alternating with the first. These secondary rays indicate the beginning of the division of each placenta along its median plane; this bisection separates the half-placentae belonging to adjacent carpels, which, up to this level, have been united. It is the faces parted by this cleavage which bear the receptive papillae (Fig. 2, C5 and C6); they form the paired stigmatic rays of which an external view is given in Fig. 2, D.

In correlation with the splitting of the placenta, the fused marginals divide—each half passing to the carpel to which it belongs. This change takes place between Fig. 1, B5 and B6, but the vascular tissue is so embryonic in this series of sections that the process is difficult to follow. It can be

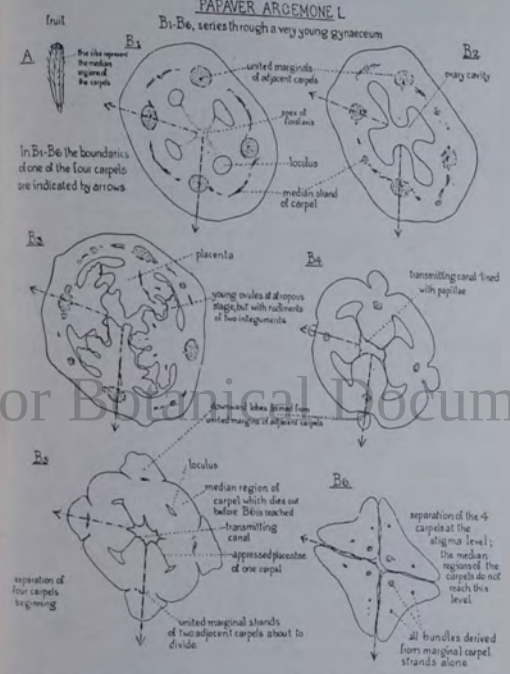

Fig. 1. (The orientation of the gynaeceum in relation to the rest of the flower is not indicated in any of the figures in this paper. All the series of sections are traced from below upwards.) *Papaver Argemone* L. A, fruit (× 1 *circa*). B1–B6, sections from a transverse series through a very young gynaeceum, Histon, 27 May 1930 (× 47). In each diagram arrows define the margins of one of the four carpels. B1, extreme base of gynaeceum; B6, the four stigmatic members.

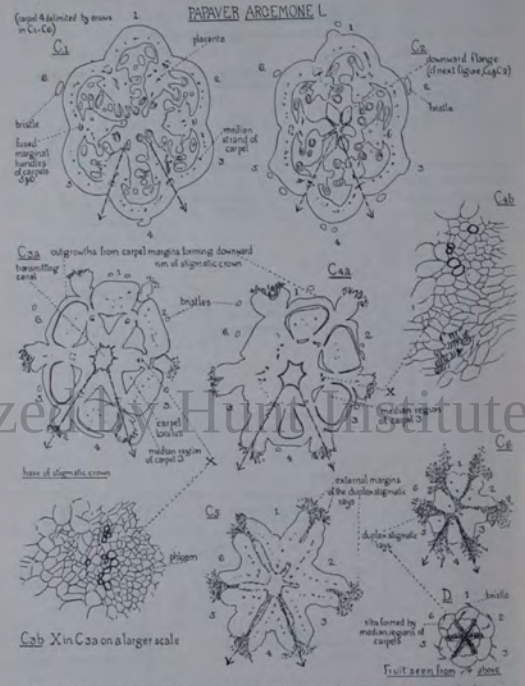

FIG. 2. *Papaver Argemone* L. C1–C6, sections from a transverse series through the gynaeceum of an unopened bud, Camb. Bot. Gard., 25 June 1936 (×14, except C3*b* and C4*b*, which are ×193 *circa*). For convenience of description the conventional numbering, 1–6, is used for the carpels, and carpel 4 is delimited by arrows. The series ranges from the fertile region of the carpels, C1, to the stigmatic members, C6. D, fruit seen from above as a solid object (enlarged).

C1 B4 - I - 10
C2 B3 - III 10
C3 B2 - I - 5
C4 B2 - I - 8
C5 B2 I - 5
C6 B1 IV - 5

traced in detail, however, in the series through the older gynaeceum drawn in Fig. 2. The upper sterile regions of the placentae in the base of the stigmatic crown are seen in Fig. 2, C3*a*; the bundles to the right of the diagram each show one xylem group, while in two of those to the left (which, owing to a slight obliquity in the section, are cut at a higher level) division is taking place. One of the individual bundles, X, is drawn on a larger scale in C3*b*. In C4*a*, which is a little higher in the gynaeceum, division is proceeding, and the result is seen in detail for bundle X in C4*b*; the xylem now forms two separate groups. The completion of these divisions represents the entire disengagement of the vascular system of each carpel from that of its neighbours, and in Fig. 1, B6, and 2, C5, each of the terminal members is seen to possess its own arc.

We have now traced the derivation of these stigmatic members, and their vascular supply, each from a single carpel; in Fig. 2, D, they are seen in external view, each standing above the median region of the carpel to which it belongs. They do not, however, each represent a whole carpel, but they are formed exclusively from its margins and placental outgrowths, which extend above, and arch over, the reduced median regions. The disappearance of the median regions of the carpels, and of the loculi, as the stigmatic crown was reached, was observed in outline in the young gynaeceum of the series in Fig. 1, B, but for a better demonstration we must go to the older series in Fig. 2. The condition in the main part of the ovary can be seen in Fig. 2, C1 and C2. In C3 we are reaching the base of the stigmatic crown, and the median regions of the carpels are reducing in width, but increasing in depth from back to front. The bundles are now scattered instead of forming a single series; in C4*a*, in carpels 1 and 2 the number of bundles is reduced, and in carpels 3 and 4 their upper limit is passed, so that there are no longer any to be seen. In this diagram, in carpels 1, 2, and 3, which are cut at a lower level than the rest, the attachments of the median regions to the placentae are narrowing, and withdrawing towards the centre of the gynaeceum, thus reducing the loculi. In carpel 4 this process has gone so far that the loculus has vanished, and the median region of the carpel is attached by the middle line of its ventral surface to the infolded and fused margins of its two half placentae; and in carpels 5 and 6 these marginal outgrowths have closed in a hood-like manner over the apex of the median region, so that it is no longer visible. As the loculi disappear, the marginal regions of the carpels thus take on an exaggerated development; they not only form the stigmatic crown itself, but also the outgrowths which produce the basal rim seen in transverse section in Fig. 2, C3*a* and C4*a*, and in longitudinal section in Fig. 3, A1 and A2.

Before leaving *P. Argemone* we may notice one point of minor importance. This is the occurrence of downwardly directed flanges from the sterile regions of the placentae high in the ovary. These can be seen cut transversely in Fig. 2, C2. The obliquity of the section reveals, on the left, two flanges continuous with the fertile placentae, and, on the right, four flanges cut in their free regions. The same structures can be seen in longitudinal section in Fig. 3, A1 and A2.

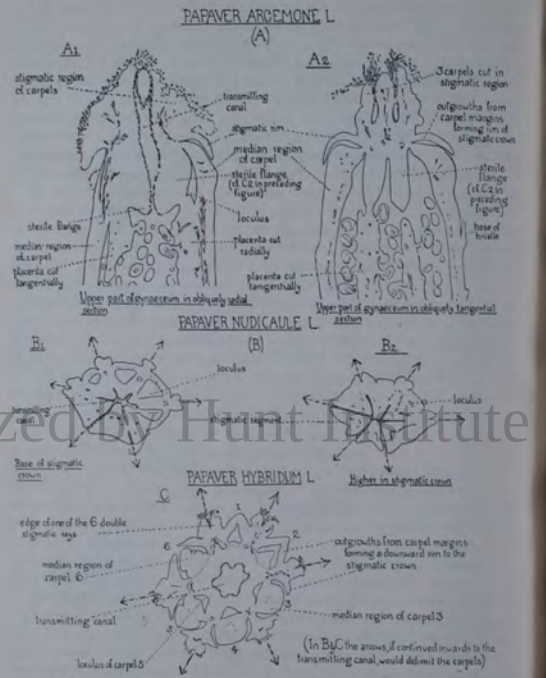

FIG. 3. A1 and A2, *Papaver Argemone* L. Sections from a slightly oblique longitudinal series through the upper part of a gynaeceum from an unopened bud, Camb. Bot. Gard., 25 June 1936 (×14). A1, approximately radial; A2, tangential. B1 and B2, *P. nudicaule* L., sections from a slightly oblique transverse series through a young gynaeceum at the stage at which differentiation of the ovule integuments has only just begun. Camb. Bot. Gard., 3 Aug. 1928 (×14). Here, and in C (below), the arrows, if continued back to the transmitting canal, would delimit the carpels. C, *P. hybridum* L., section at the base of the stigmatic crown from a transverse series through a gynaeceum, Camb. Bot. Gard., 28 July 1928 (×14).

A1. A2 I-1
A2 A2. II 1
C. B2 II 1

Serial sections of the gynaecea of *Papaver nudicaule* L., *P. hybridum* L., and *P. Rhoeas* L. were cut for comparison with *P. Argemone*; they were found to agree with this species in all essential points. Fig. 3, C, passes through the base of the stigmatic crown in *P. hybridum*. Being slightly oblique, it shows the vascular median regions of carpels 3, 4, and 5, with the loculi on their inner faces, while in carpels 6, 1, and 2 the upper limits both of the loculus and of the vascular tissue of the median carpellary region have been passed. It will be seen that the ventral (inner) faces of the median regions of these three carpels are, at this level, united with the stigmatic crown. The arrangement of the elements makes it possible to distinguish the tissue of the median region of the carpel from the tissue of the marginal regions, and this boundary is indicated for these three carpels by dotted lines; but there is perfect tissue-continuity between the tips of the median regions of these carpels and the stigmatic crown. Fig. 3, C, also shows the development of the stigmatic rim, and the early stages in the division of the placentae and their bundles. In this diagram, and in those of *P. nudicaule* (B1 and B2), the arrows, if carried inwards to the transmitting canal, would mark the boundaries between adjacent carpels.

The sections of *P. Rhoeas* drawn in Fig. 4 may be used to illustrate certain special points which were not demonstrated for *P. Argemone*. One of these is the history of the vascular structure in the base of the gynaeceum and in the placentae. Fig. 4, A1, is cut at a level at which the bundles of the uppermost stamens have not yet left the axis. The central cylinder has ten residual bundles, which are perfectly distinct as regards their lignified xylem, but which form a ring by a continuity which chiefly concerns the phloem and the sheath tissue. In A2*a* we pass into the stalk of the gynaeceum, which corresponds, on a small scale, to the gynophore of the Capparidaceae. The ten residual bundles are now free from one another, and there is no vascular tissue between them. In A2*b* (the bundle x in A2*a* on a larger scale) we find that, outside the sheath cells, which are large, with highly stainable walls, there are groups of active elements, rich in contents, which, at a higher level, will give rise to vascular strands. Similar groups are seen in E1*b* and E2. In A3 the bundles for the gynaeceum are already marked out. Between the ten lignified bundles (which are the fused marginals of adjacent carpels, from which the placental supply will originate) there are extremely delicate non-lignified strands for the main regions of the carpels. These strands arose *de novo* in the parenchyma, and at this level they are not connected with the fused marginals. In A4 we come to the first appearance of the carpel loculi, which surround the vestigial non-vascular apex of the floral axis; sections showing this feature have been obtained from four other gynaecea. Fig. A5*a* is cut at 70μ above A4, but below the fertile region of the ovary. The groups of active cells, belonging to the surface tissue of the bundles, which were noticed in A1*b*, are now giving rise to unlignified strands which connect with the bundles of the median regions of the carpels—also at this level unlignified.

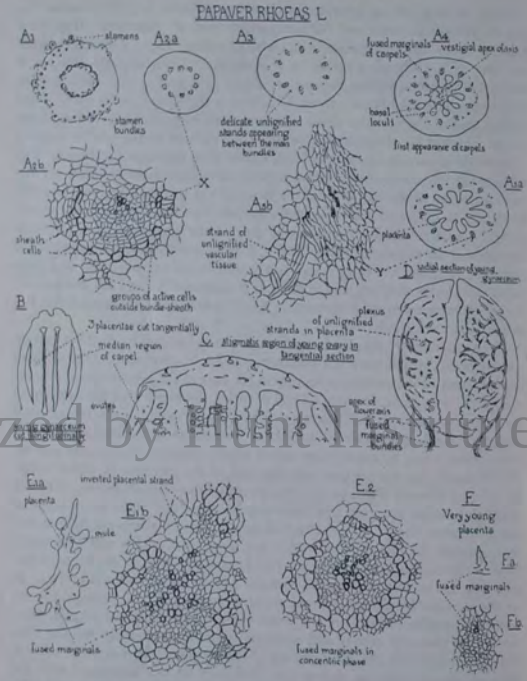

FIG. 4. A–D, *Papaver Rhoeas* L. A1–A5, sections from a transverse series through the lower part of the gynaecceum of an unopened bud, gravel pit, Camb. Univ. Farm, 24 May 1936 (×14, except A2*b* and A5*b*, which are ×193 *circa*). A1, level at which there are still stamen bundles in the floral axis. A2*b*, bundle X in A2*a* on a larger scale. A4, actual base of gynaecium. A5*a*, sterile bases of placentae. A5*b*, bundle Y in A5*a* on a larger scale. B, longitudinal section from a series through a very young ovary, Whittlesford, 28 May 1936 (×23). Three placentae are cut tangentially, and the median regions of two carpels are cut more or less radially. The gynaecium is so young that no ovules have yet been produced. The shaded edges of the placentae represent the border of cells rich in protoplasm from which the ovules will be

(A1). C11. II 3
(A2) C11-I 16,7
(A4) C11 II-3 6
(A5) C11 . II
(B.) P2 I 1
(C.) M2
(D.) N3. II-3
(E1) C II 6
(E2) C II 6
(F.) U2. J. 6

The fused marginals are slightly oblique. Fig. A5*b* shows one of these bundles, Y, on a larger scale; it is giving off an unlignified branch to the south-west.

Even in extremely young ovaries of *P. Rhoeas*, from the base the fused marginal strands tend to be slightly concentric (Fig. 4, F*b*). In older stages this feature is emphasized, the xylem being placed centrally with the phloem surrounding it, and the sheath closing more or less completely round the bundle (Fig. 4, E2). The result is that when a strand from such a bundle is given off towards the placenta, the phloem of the branch bundle is naturally turned towards the placenta and the xylem towards the parent bundle (Fig. 4, E1*a* and E1*b*).

The nature of the vascular system within the placenta cannot be understood from transverse sections, but its general scheme is shown in Fig. 4, D, which is a radial section through a gynaecceum so young that the rudimentary ovules have not yet produced integuments. It will be seen that a very elaborate plexus of strands arises from the fused marginal bundles and penetrates the tissue of the placenta. At the stage figured there is little lignification except in the main bundles.

The tissue-continuity between the median regions of the carpels and the stigmatic crown has already been demonstrated in transverse sections of *P. Argemone* and *P. hybridum*. In Fig. 4, B and C, longitudinal sections of a young gynaecceum of *P. Rhoeas* are drawn to show this continuity from a different aspect; it is only at a later stage that it is interrupted by the formation of the dehiscence pores.

The two genera most nearly allied to Papaver are Argemone and Meconopsis. Serial sections of the gynaecceum of *Argemone mexicana* L. are illustrated in Fig. 5, A1–A9, and the stigmatic crown is shown as a solid object in C1 and C2. The general structure is essentially similar to that of Papaver, so our description may be limited to the vascular supply, in which certain critical features can be seen more clearly than in Papaver. In the A series in Fig. 5 the bundle X and its products are marked in each diagram, so that its history can be followed into the stigma. As compared with Papaver, the placentae in the fertile region of the ovary, and the base of the apical sterile region, project little into the cavity (Fig. 5, A1), and the vascular supply for the placenta scarcely becomes detached from the fused marginals. A2*a* and A2*b* in Fig. 5 show two inverted bundles given off on the placenta side, which have remained

developed. C, tangential section from a series through the top of a gynaecceum, Whittlesford, 28 May 1936 (×14); the ovules are so young that they are still atropous, but rudiments of both integuments have appeared. D, approximately radial section from a longitudinal series through a young gynaecceum, Whittlesford, 28 May 1936 (×14); the ovules have not yet developed the rudiments of integuments. E1*a*, one placenta from a transverse series through the gynaecceum of an open flower, gravel pit, Camb. Univ. Farm, 24 May 1936 (×14). E1*b*, fused marginal strands from E1*a* (×193 *circa*). E2, fused marginals associated with another placenta in the same section as E1; this bundle is not, at the moment, giving off a strand to the placenta in the same section as E1; this bundle is not, at the moment, giving off a strand to the placenta (×193 *circa*). F*a*, one placenta from a transverse series through the gynaecceum of an unopened bud, gravel pit, Camb. Univ. Farm, 24 May 1936 (×14). At this very young stage the ovules are mere prominences. F*b*, fused marginals of F*a* (×193 *circa*).

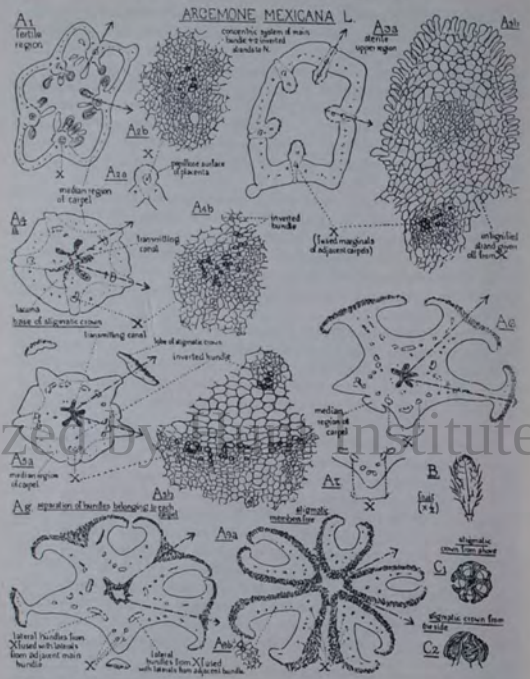

FIG. 5. *Argemone mexicana* L., Camb. Bot. Gard., 13 July 1936. A1–A9, sections from a transverse series through the upper part of a gynaeceum; one carpel is delimited by arrows. A1, fertile region of ovary (×14). A2*a*, a placenta cut at a slightly higher level where it is sterile (×23). A2*b*, fused marginal bundles in A2*a* (×193 *circa*). A3*a*, upper sterile region of ovary (×23). A3*b*, placenta and bundle X (×193 *circa*). A4*a*, extreme top of ovary where it passes into stigmatic cap; section slightly oblique, and one lacuna only seen (×23). A4*b*, X in A4*a* (× 193 *circa*) to show an inverted bundle being given off. A5*a* passes through apices of median regions of carpels, above the tips of the vascular bundles of three of them (×23). A5*b*, X in A5*a* (×193 *circa*); the main bundle is spreading and dividing, and the inverted bundle has been detached. A6, base of stigmatic crown (×23). In A6 and A7 all the bundles within the bracket are derived from X. A7, further division of X (×23). A8 and A9*a* (×23). A9*b*, one of the bundles in A9*a* (×193 *circa*) to show that the xylem is turned towards the papillose surface. B, fruit (×½). C1, gynaeceum as a solid object seen from above. C2, a similar stigmatic crown seen from the side. C1 and C2, both enlarged and prickles removed.

(A1) B2.I-1 (A8) B4-II-10
(A2) B3 I 11 (A9) B4-II-5
(A3) B3-I-1
(A4) B4. II. 7
(A5) B4. II. 6
(A6) B4. II 5
(A7) B4-II-10

in contact with the fused marginals to form a concentric plexus. In the higher sterile region of the ovary, however, an unlignified strand passes into each placenta (Fig. 5, A3*a* and *b*), while, in the base of the stigmatic crown, corresponding bundles, which are lignified and show inverted orientation, move away to some distance from the fused marginals (Fig. 5, A5*a* and *b*). In A6–A9 the process in which X shows its compound character can be followed; its components become distributed between the adjacent carpels to which they belong. In the stigmatic members the xylem of each bundle is directed towards the papillose surface (A9*b*).

Meconopsis is slightly modified from the Papaver type by the fact that the stigmatic crown is raised on a style. A few sections from a series through the distal portion of a gynaeceum of *M. aculeata* Royle are drawn in Fig. 6. The upper sterile parts of the placentae are shown in Fig. 6, A1. The tip of the median region of each carpel has a slight 'shoulder' at its attachment to the style; two of these projections are cut in their free region in A2. A3 passes through the style, and it is seen that the central transmitting canal has four arms *in the median planes of the carpels*. A4 is higher in the style; at this level the sectional form of the transmitting canal has changed, and it now shows four arms *in the planes between the carpels*. These arms are the first indications of the disjunction of the four carpels. In A5 we reach the stigmatic region in which the separation of the four carpels is complete.

III. Discussion

In contrast with the theory of the gynaeceum of Papaver generally used by systematists, which has been applied to the minute structure in the preceding pages, another view, sponsored by Kerner and Oliver (1895), has been revived in recent years by Saunders (1930), &c., and Dickson (1935). According to this view the parts which are called in the present paper the median regions of the carpels, are interpreted as an outer whorl of sterile carpels, while the placentae represent an inner whorl of fertile carpels. Some of the evidence adduced by Dickson, who has given the most detailed exposition of this theory, must now be considered. In certain critical points the observations in the present paper differ somewhat from those recorded by that author. She states that in Papaver the 'expanded carpels' [median regions of the carpels, in the terminology used here] '*are never fused with the stigmatic disc*, for the disc can always be dissected from the capsule without causing any injury to the tips of the expanded carpels. Specimens at every stage of growth were examined, and this was always so in *Papaver Rhoeas, P. Argemone, P. hybridum, P. somniferum, P. orientale, P. bracteatum*.' Such

observations might be held to support the idea that the placentae, and the median regions of the carpels, belong to different members; it may be doubted, however, whether it is safe to base negative conclusions about tissue connexions upon evidence of this type. The sections figured in the present

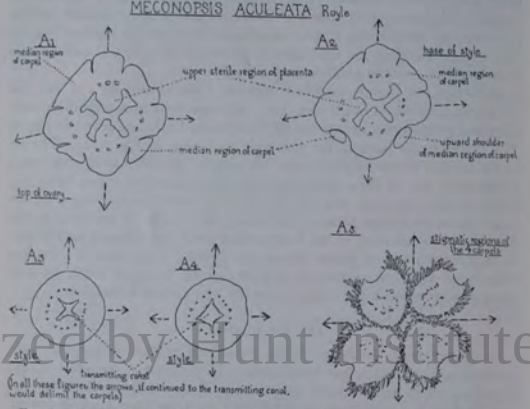

FIG. 6. *Meconopsis aculeata* Royle. Sections from a transverse series through the upper part of a gynaeceum, Camb. Bot. Gard., 26 June 1936 (×23). The arrows in each diagram, if carried to the transmitting canal, would delimit the carpels.

paper show that in the young gynaeceum of *P. Argemone* (Fig. 2, c4*a*, carpel 4; Fig. 3, A2), *P. hybridum* (Fig. 3, C, carpels 6, 1, 2), and *P. Rhoeas* (Fig. 4, B and C) there is *perfect tissue-continuity* between the median region of the carpel and the stigmatic crown. At these young stages the stigmatic crown could be removed only if the delicate connexions were torn away; in the process of dissection such tearing might easily happen without being perceptible. Again, in describing the stigmatic structure, Dickson states that 'the vascular bundles of the contracted carpels' [the fused carpel margins with their placental outgrowths, in the terminology used here] 'remain unchanged throughout their course. When they reach the top of the ovary-wall they bend inwards, almost right angles, and run along underneath the stigmatic rays.' This, as it stands, might also be accepted as evidence for the interpretation of the marginal and placental regions as distinct carpels, but a different picture is given by the observations described in the present

paper. In my preparations the fused marginal bundles do not 'remain unchanged throughout their course', but each invariably separates into two halves in the base of the stigmatic region, one half passing into the stigmatic member on either hand. This is illustrated for *Papaver Argemone* in Figs. 2, c3*a* and *b*, c4*a* and *b*; while the process can be followed more easily for *Argemone mexicana* in Fig. 5, in which the bundle x can be traced throughout the A series.

In recent theories of the constitution of the gynaeceum in the Cruciferae and Papaveraceae, stress has been laid on the inverted character of the bundles supplying the placentae, and their orientation has been accounted for by supposing them to be the ventral strands of the 'contracted carpels' (e.g. Dickson, 1935). The inversion of these strands can, however, be explained quite simply on mechanical grounds. It must be remembered that each placenta is immediately internal to one of the strands which are here interpreted as fused marginals. Exactly how such a strand can supply bundles to the placenta, which is on its own radius, is a special case of the general problem of how a collateral bundle can give off a branch on its xylem side. In *Papaver Rhoeas*, as we have seen, this problem is solved by the bundle becoming concentric (Fig. 4, E2); when a portion of it is detached on the side towards the placenta, it thus naturally has its xylem turned towards the parent strand, and its phloem away—in other words, it is 'inverted' (Fig. 4, E1*b*). The same thing occurs in *Argemone mexicana*, but here the inverted strands tend to remain associated with the fused marginals to form a concentric plexus (Fig. 5, A2*a*, A2*b*), though in the base of the stigmatic cap they may become free (A4*a*, *b*; A5*a*, *b*).

The occurrence of 'inverted' bundles in the placentae is only one of the aberrant results that may follow when one collateral bundle has to supply a vascular system for a structure internal to itself on the same radius of the shoot. It has been shown in a previous paper (Arber, 1932; see also 1937*a*) that the two-bundled character of the stamen filaments in Hypecoum—which has sometimes been interpreted as indicating that these stamens represent an ancestral pair—is also due merely to a special type of bundle-branching associated with the superposition of a stamen upon a petal.

It will, I think, be recognized from the descriptions and figures in the preceding section of this paper that the gynaeceum of Papaver can be described in a consistent fashion on the theory that it is formed from a single whorl of carpels, all of the same type, and bearing ovules on placental outgrowths from the united margins of adjacent members. On analysis, the peculiarities of the Papaver gynaeceum are all found to arise out of the reduction of the median region of each carpel, and the corresponding overgrowth of its margins. The carpel shows that 'sorte de tendance à la trilobation' detected by Lignier (1911) in the gynaeceum of Glaucium. The median regions of the carpels in Papaver do not extend to the apex of the gynaeceum, but are completely overarched at the tip by a hood formed from the marginal regions. The

vascular system of the median region is reduced in correspondence with the external reduction, while the fused marginal bundles are highly developed in correlation with their function as the supply channels for the ovule-bearing placentae.

Within the Papaveraceae it would be hard to find a genus with gynaeceum structure more remote from that of Papaver than Platystemon. We have

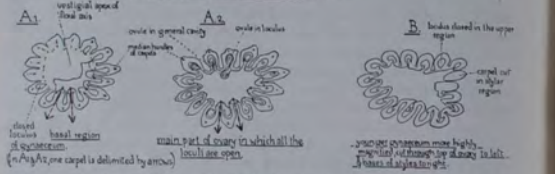

FIG. 7. *Platystemon californicus* Benth., Camb. Bot. Gard., 5 June 1936. A1 and A2, sections from a slightly oblique transverse series through a gynaeceum (×14). B, section from a slightly oblique transverse series through a very young gynaeceum, showing to the right the base of the stylar region (×23).

shown that the theory here adopted gives a consistent explanation for Papaver, when this genus is considered in itself, and now—as a further test of the efficiency of the theory—we will apply it to the comparison of Papaver and Platystemon. In the base of the ovary of *Papaver Rhoeas* (Fig. 4, A4) the carpels, which at their first appearance have closed loculi (cf. also Fig. 1, B1), surround the vestigial apex of the floral axis. Such sections may be compared closely with that of *Platystemon californicus*, cut at a corresponding level, which is drawn in Fig. 7, A1. If the marginal bundles of adjacent carpels were united, and the ovules were borne on a placental outgrowth from the fused margins, we should arrive at a scheme of structure recalling Papaver. Fig. 7, A2, with its open loculi, if it were so modified, might be compared with the section of *Papaver Argemone* drawn in Fig. 2, C1. Fig. 7, B, is cut through the upper part of a very young ovary of Platystemon, and we see that, just before the carpels become stylar, the loculi repeat the closure which we noticed in the base. This closure of the loculi at the tip of the ovary can be paralleled in Papaver. The stigmatic members of Platystemon, like those of Papaver, are each formed from a single carpel only; but those of Platystemon differ from those of Papaver in incorporating the median as well as the lateral regions of the carpel. We thus see that, though at first glance the gynaeceum of Papaver seems remote from that of Platystemon, the fundamental relation of these superficially dissimilar types becomes clear when they are considered in the light of the theory here adopted.

IV. Summary

This study is based upon serial sections of the gynaecea of *Papaver Argemone* L., *P. Rhoeas* L., *P. hybridum* L., *P. nudicaule* L., *Argemone mexicana* L., *Meconopsis aculeata* Royle, *Platystemon californicus* Benth., and other Papaveraceae. It is shown that the minute structure offers no support to the hypothesis that the gynaeceum of Papaver includes two types of carpel—sterile and fertile (see also Arber, 1937*a*). On the contrary the evidence favours the view that the gynaeceum consists of a single whorl of carpels, which are identical in type, and are equal in number to the placentae, and to the duplex stigmatic rays. In the ovary adjacent carpels are fused marginally, and the placentae represent outgrowths from these united edges; the placentae are thus duplex in origin. The inverted bundles of the placentae owe their inversion to an anatomical necessity; in morphological argument no stress, therefore, can be laid on this peculiarity. The carpels separate in the stigmatic crown by the splitting of each placenta along its median plane. The fused marginal bundles divide, and their components are distributed to the carpels on either hand to which they belong. The free surfaces produced by the splitting of the placentae bear papillae; each stigmatic ray hence represents the adjacent faces of two carpels. The median regions of the carpels are much reduced and take no part in the formation of the stigmatic crown. It is not, however, until a relatively late stage that the apices of the median regions of the carpels break away from the base of the stigmatic crown, thus forming the dehiscence pores. Each stigmatic member stands directly above the median region of the carpel to which it belongs; it is formed exclusively from the marginal and placental regions of that carpel, which overarch the reduced median region.

The structure in the allied genera Argemone and Meconopsis differs in no essential respect from that in Papaver.

A comparison with Platystemon—chosen as the member of the Papaveraceae in which the gynaeceum differs most obviously from that of Papaver—shows that the theory outlined above makes it possible to relate these two extreme types, and thus to bring the gynaeceum structure of the Papaveraceae under a unified conception.

Literature Cited

Arber, A., 1932: Studies in Floral Morphology. IV. On the Hypecoideae with special reference to the Androecium. New Phyt., xxxi. 145–73.

—— 1937: Studies in Flower Structure. III. On the 'Corona' and Androecium in certain Amaryllidaceae. Ann. Bot., N.S. i, 293–304.

—— 1937*a*: The Interpretation of the Flower: a Study of Some Aspects of Morphological Thought. Biol. Rev., xii. 157–84.

Candolle, A. P. de, 1827: Organographie Végétale. Paris.

PRINTED IN GREAT BRITAIN AT THE UNIVERSITY PRESS, OXFORD
BY JOHN JOHNSON, PRINTER TO THE UNIVERSITY

ARBER, A.

STUDIES IN FLOWER STRUCTURE

V. ON THE INTERPRETATION OF THE PETAL AND 'CORONA' IN LYCHNIS

Reprinted from Annals of Botany
New Series Vol. III No. 10 April 1939
Pages 337–346

Printed in Great Britain

Lychnis studies: white box 50; flax box 9; box 8 (1937)
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Studies in Flower Structure

V. On the Interpretation of the Petal and 'Corona' in Lychnis

BY

AGNES ARBER

With five Figures in the Text

I. Introduction

THE work detailed in the present paper was undertaken with two objects. The first of these was to try to throw light upon the nature of the outgrowths borne by the petals of Lychnis. The second was to see whether the structure of the flower in this genus could be regarded as compatible with the theory recently enunciated by Mattfeld (1938, 1938*a*), according to which the petal of the Caryophyllaceae is a duplex member, representing paired stipular appendages belonging to the stamen with which it is associated. In the following pages these two problems will be considered separately.

II. The 'Corona' of Lychnis

(i) *Observations*

The male flower of *Lychnis vespertina* Sibth. may be taken as a convenient type in which to study the corolline outgrowths. Fig. 1A, p. 338, shows one of the petals with four outgrowths at the junction of claw and limb—two very delicate lateral wings, with two less fragile coronal teeth between them. In material collected near Cambridge, the coronal teeth have been found to be better developed in the male flower; in the female they tend to be rudimentary (Fig. 1, B). The corolla structure is variable, however, and suggests that the species might repay a study dealing analytically with the distribution and relation of the sexes, and with the characters—sex-linked or not—which distinguish the different forms.

[Annals of Botany, N.S. Vol. III. No. 10, April 1939.]
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Fig. 1, A, is drawn from a fresh petal, but C and D from petals stained whole to show the general vascular system of claw and limb. There are a median bundle and two laterals in the claw, while in the limb a network is produced by the branching of these three main strands. The median bundle bifurcates below the indentation of the limb. Preparations of the whole petal, such as

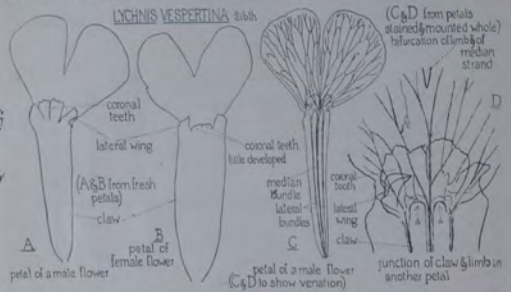

Fig. 1. *Lychnis vespertina* Sibth. A, petal of a male flower (×2½). B, petal from a bud (female) on the point of unfolding (×2½). C, petal of a male flower stained whole in gentian violet and eosin, and viewed from the front (×2½). D, junction of limb and claw from another petal treated as in C (×6 *circa*). This treatment shrinks the lateral wings and coronal teeth and renders them transparent; they can be better seen in A and B, drawn from fresh petals. The dotted arrows in D mark the mouths of the invaginations forming the coronal teeth.

those drawn in C and D, are not suitable for detailed examination of the outgrowths; for this purpose recourse must be had to transverse microtome series, such as those illustrated in Figs. 2, p. 339, and 3, p. 340. The junction of claw and limb in a single petal can be studied in Fig. 2, A1–A8, while further details of the formation of the corona are shown in Fig. 3. The delicate non-vascular wings are in process of detachment in Fig. 2, A2 and A3, and are completely free in A4–A8. In outline drawings of sections, such as those in Figs. 2 and 3, the wings are liable to look more substantial than they are in the living state, since the delicate mesophyll tears easily, and the upper and lower epidermal layers thus become too widely separated from one another.

At and above the level of detachment of the wings, two longitudinal wrinkles are formed in the petal limb, one on either side of the midrib, with a corresponding groove below each (Fig. 2, A3). On the upper surface the two wrinkles are separated by a narrow median groove, immediately above the midrib. If this midrib groove is followed downwards, its faces are found to fuse so as to leave an internal cavity (Fig. 2, A2, and B). The adjacent faces of the lateral grooves also fuse with one another at a level a little above their

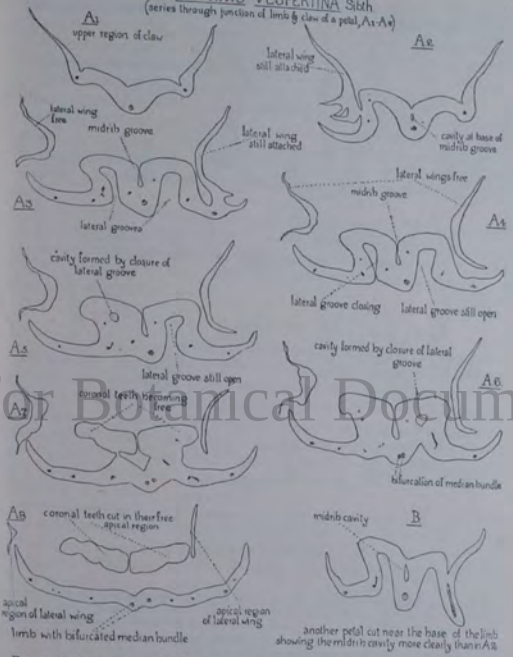

Fig. 2. *Lychnis vespertina* Sibth. A1–A8, sections from a transverse series from below upwards through the junction of limb and claw of a petal of a male flower (×23). B, transverse section of another petal from the same flower as the A series, cut near the base of the limb. (×23).

origin, leaving a small cavity within; this fusion has occurred on the left-hand side, but not on the right-hand side, in Fig. 2, A5. The crown of each wrinkle, with its hollow centre, is prolonged upwards to form a free coronal tooth (Fig. 3, C3 and C4, p. 342). We may thus say that at the junction of claw and

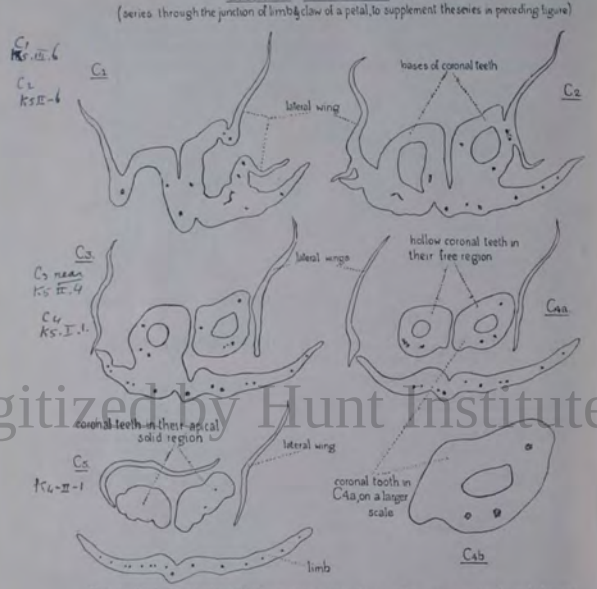

FIG. 3. *Lychnis vespertina* Sibth. C1–C5, sections from a transverse series from below upwards through a petal of a male flower (×23, except C4*b*); slightly damaged on the left-hand side of the petal, and reconstructed. C4*b*, shows one of the coronal teeth in C4*a* (×47); the xylem elements are indicated individually. (In this petal the attachment of the left-hand lateral wing is peculiar; the series cannot be followed below C1.)

limb there are three invaginations: the smallest of these is over the midrib, and opens in the upward direction on to the ventral surface of the petal, while the other two are lateral, and open in the downward direction on to the dorsal surface of the petal, in the positions marked with arrows in Fig. 1, D, p. 338. These lateral invaginations are continued upwards as free teeth projecting from the inner face of the petal, hollow below (Fig. 3, C4*a*), but solid at the

apex (Fig. 2, A8, and 3, C5). The teeth are only slightly supplied with vascular tissue, and such bundles as enter them die out before their tips are reached (*cf.* Fig. 2, A7 and A8). The external surface of each tooth belongs entirely to the upper petal surface, and the xylems of the bundles are all, as would be expected, directed towards this face (Fig. 3, C4*b*).

The construction of the coronal teeth is perhaps not easy to visualize from a description of sections; it may make it clearer if we imagine an enlarged version of the petal made of some extensible material which can be moulded at will, and suppose that two fingers are pressed into the back of the petal at the base of the limb—one on either side of the midrib—so as to force the petal into two glove-finger-like protrusions. These would represent the coronal teeth.

Lychnis vespertina is the only species of which I have cut microtome series through the coronal teeth. I have, however, cut hand sections of the petals of *L. diurna* Sibth. (male form) and *Silene maritima* With., and I have found that in both these species the coronal outgrowths conform to the same type as those of *L. vespertina*.

(ii) *Discussion*

The two kinds of outgrowth at the junction of claw and limb in Lychnis—'lateral wings' and 'coronal teeth'—must be distinguished sharply from one another (cf. Velenovský, 1910); their structure, as shown in Figs. 2 and 3, is wholly different. The delicate, non-vascular lateral wings may be interpreted without special difficulty, for there seems no reason against comparing them with stipules. Glück (1919, pp. 92, 327) has pointed out that certain stipules of foliage leaves may be without vascular bundles, and illustrations of the non-vascular stipules of *Nasturtium officinale* R. Br. will be found in Arber, 1931, Fig. 8, p. 186.

The coronal teeth, on the other hand, are more problematic. They have generally been classed as ligular (e.g. Eichler, 1878; Pax, 1889; Glück, 1919; Rendle, 1925), and it has also been suggested that they may possibly prove to be stipular (Woodson and Moore, 1938). Velenovský (1910), on the other hand, regarded them as outgrowths whose orientation was opposite to that of the petals from which they arose; they would thus be comparable with the enation corona of Narcissus (cf. Arber, 1937). These three theories are all based on the supposition that the coronal tooth is a bifacial member, with an upper and a lower surface; if it is ligular or stipular, it should have its dorsal surface turned towards the ventral (upper) surface of the petal, and, if it is an enation, it should have its ventral surface turned towards the ventral surface of the petal. The observations recorded in the present paper demonstrate, however, that the tooth is not bifacial at all, since its free surface belongs exclusively to the *upper* surface of the petal; it represents a dorsal invagination of the petal, and can thus be neither ligular, stipular, nor an enation. These three possibilities being ruled out, the question arises as to whether there is

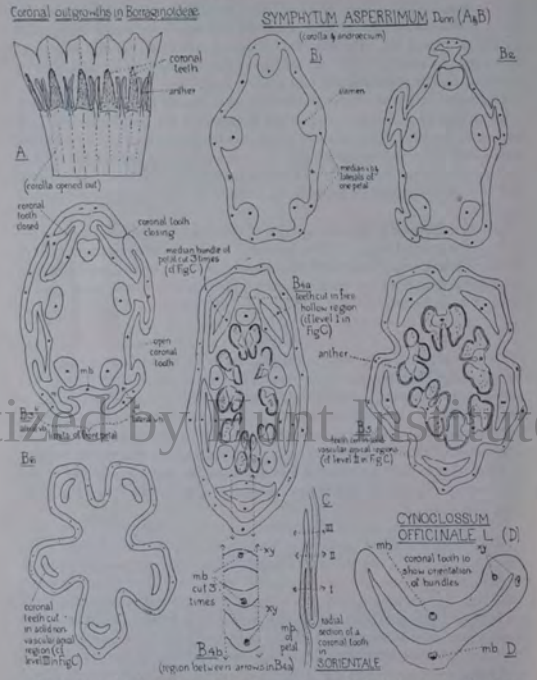

FIG. 4. Coronal teeth of Borraginoideae for comparison with Lychnis. A and B, *Symphytum asperrimum* Donn. A, corolla opened out (×2½ *circa*), showing the coronal teeth with their papillose margins, opposite the petals; they are dotted for distinctness. B1–B6, sections from a transverse series from below upwards through a young flower (×14, except B4*b*); only corolla and androecium are included. B4*b*, sketch on a larger scale of the region between the arrows in B4*a*, to show the orientation of the median bundle, which is cut three times. C, *Symphytum orientale* L., radial longitudinal section of a coronal tooth from a series through a corolla (×14); the centre of the flower would be to the left. The median bundle of the petal is dotted. D, *Cynoglossum officinale* L., transverse section of a coronal tooth cut in its free region, to show the orientation of the vascular bundles (×47); the centre of the flower would be to the north.

any descriptive category to which these coronal teeth can be assigned. The closest parallel which I have been able to find for them is with the teeth (Hohlschuppen) in the mouth of the corolla tube of the Borraginoideae (cf. Gürke, 1897, and Brand, 1921, 1931). For comparison with Lychnis I have cut microtome series through the corollas of *Caccinia glauca* Savi, *Cynoglossum officinale* L., *Symphytum asperrimum* Donn, *S. orientale* L., *Pulmonaria officinalis* L., and *Myosotis palustris* Lam. The construction of the corona in all these species is essentially similar; like those of Lychnis, the teeth are hollow invaginations (Einstülpungen) of the petal from the lower surface, ending in a solid apex. Their external appearance is shown in Fig. 4, A, p. 342; their structure will be understood from B1–B6, which represent transverse sections from a series through a corolla, passing from below upwards from the region in which the filaments are fused with the tube, to the tips of the coronal teeth. The teeth differ, however, in certain important respects from those of Lychnis. Each petal, instead of bearing *two lateral teeth* with little vascular tissue (as in Lychnis), bears *one median tooth* supplied by the median bundle itself, which passes up from the corolla tube within the inner wall of the tooth to its apex, then runs down within the outer wall, and then up again into the free part of the petal. This upward, downward, and upward course of the median bundle can be followed in transverse sections in Fig. 4, B1–B6, and in longitudinal section in C.

This comparison between the coronal teeth of members of the Silenoideae and Borraginoideae is made without any idea of suggesting a taxonomic relationship between plants belonging to widely different cycles of affinity. Types of structure, as such, may stand in a close morphological relation, which is wholly independent of phylogeny.

III. The Nature of the Petal in the Caryophyllaceae, and the Meaning of Obdiplostemony

The connexion between the petal and its superposed stamen, in the Caryophyllaceae, is a striking feature to which attention has often been drawn in the literature. Recently a theory of the nature of the corolla in the Caryophyllaceae and other families—based upon the intimacy of the petal-stamen connexion, and upon the relation of the episepalous stamens to the nectary tissue —has been suggested by Mattfeld (1938, 1938*a*). This author regards the glandular tissue as staminal, and as representing stipule-like basal parts of the episepalous stamens. He considers that the petals are homologues of the glands; that is to say, he regards the petals as dorsal, stipule-like basal parts of the alternisepalous stamens. Thus an episepalous stamen, together with its gland, and an alternisepalous stamen, together with its petal, each consist of one phyllome only, and are homologous. This leads to the conclusion that the Caryophyllaceae have only two whorls between the sepals and the carpels. Mattfeld founds his theory on the Alsinoideae, in which the glands are particularly well developed, but since he proceeds to apply it to the

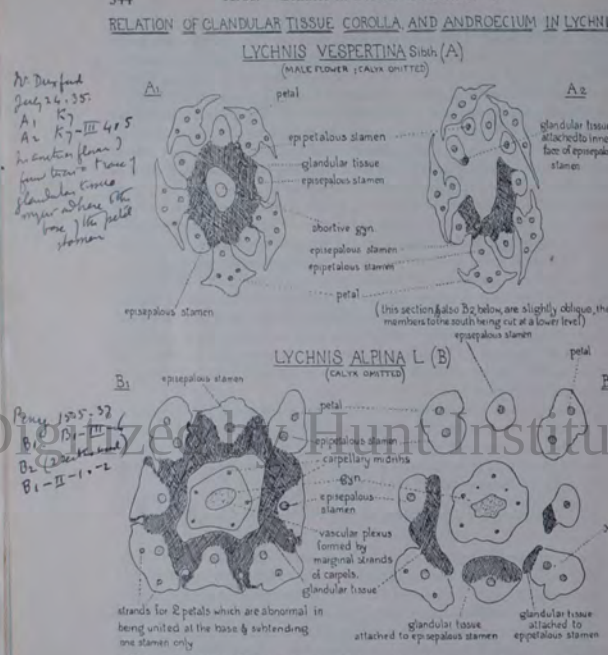

FIG. 5. A1 and A2, *Lychnis vespertina* Sibth., sections (×23) from a transverse series from below upwards through a young male flower, passing through the bases of the petals and stamens. B1 and B2, *Lychnis alpina* L. (garden material), sections (×47) passing through the bases of the petals and stamens from a transverse series from below upwards through a young flower; two sections were used in B2. Throughout this figure the glandular tissue is shaded.

Caryophyllaceae as a whole, it may fairly be tested by considering it in relation to Lychnis, a member of the Silenoideae.

In Fig. 5, A1, and also in A2, which is cut at a slightly higher level, the bases of the stamens and petals of *Lychnis vespertina* are shown; the

glandular tissue is shaded. The basal attachment of the epipetalous stamens to the corresponding petals can be seen in both figures. On Mattfeld's theory we should expect to find the glandular tissue dorsal to the episepalous stamens, as the petals are dorsal to the epipetalous stamens; but the glandular investment is seen, on the contrary, to lie on the *adaxial* faces of the stamen bases, while the petal tissue is *abaxial*. This difference in their topographical relations makes it highly improbable that petals and glands are equivalent outgrowths from the stamens. Another fact which is also irreconcilable with Mattfield's theory is indicated in Fig. 5, B2, drawn from *Lychnis alpina* L. It will be seen that, although the main part of the nectary tissue is attached to the bases of the episepalous stamens, a trace of it is carried up upon the bases of the epipetalous stamens to above the level at which the conjunct bases of petal and stamen leave the axis (e.g. the petal-stamen base marked X). The glandular tissue is thus not associated exclusively with the episepalous stamens, as it should be on Mattfeld's theory.

An unusual occurrence illustrated in the lower left-hand corner of Fig. 5, B1 and B2, is perhaps worth considering. The flower sectioned was abnormal in the fact that two of the petals were fused basally, though free at a higher level; their united bases were found to subtend *one stamen only*. This would be an unlikely contingency if the petals were stipules of the stamens, since it would mean that a single stamen could possess two pairs of stipules.

Apart from these detailed criticisms, a more general objection to Mattfeld's view is that it involves the supposition that two stipules belonging to the stamen have fused *abaxially*, i.e. behind the stamen. This author states (1938*a* p. 93) that such dorsal fusion may occur in the stipules of foliage leaves, and refers to the illustrations of *Althaea rosea* and *Hydrocotyle americana*, in Glück's book on stipules (1919), as examples in which 'die Nebenblätter der Laubblätter auf der Rückseite der Blattstiele verwachsen'. I cannot, however, detect, either in Glück's Fig. 68, p. 172 (*Althaea rosea* Cav.,) or in Fig. 79, p. 188 (*Hydrocotyle americana* L.), any indication of the dorsal fusion of stipules which Mattfeld mentions, nor can I find any reference to it in Glück's text. It seems, indeed, to be a general rule that stipular fusion, if it occurs at all, occurs in front of the rest of the leaf, and thus any interpretation must lose probability if it postulates the dorsal fusion of stipules.

Mattfeld's theory, that the petal and its associated stamen form one phyllome, has the apparent advantage that, by reducing the number of whorls recognized in the corolla and androecium, it may account for obdiplostemony in certain cases. If, however, his theory is not accepted, we can think of this obdiplostemony in still simpler terms by adopting the view that alternation of whorls is a matter of spatial and mechanical possibilities, rather than of morphological significance. In a study of the Fumarioideae (1931*a*) I pointed out that the lateral stamens belong *anatomically* to the inner whorl of the androecium, but *in the alternation sequence* they count as one whorl with the lateral petals on which they are superposed. This conclusion can be extended, with

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ARBER, AGNES

STUDIES IN FLOWER STRUCTURE

Reprinted from Annals of Botany
New Series Vol. IV No. 15 July 1940
Pages 617–628

Printed in Great Britain

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Studies in Flower Structure

VII. On the Gynaeceum of Reseda, with a Consideration of Paracarpy

BY

AGNES ARBER

Reprinted from

Annals of Botany. N.S. Vol. VI, No. 21, January 1942

Printed at the University Press, Oxford, England

the apex from youth to maturity. Special attention has also been attracted to the carpellary analysis of the genus, in connexion with Troll's theory of paracarpy. It has hence seemed worth while to re-examine the structure of the Reseda gynaeceum with these relations in mind. The theoretical questions involved will be discussed after certain relevant features in the construction have been briefly described.

2. Description

A four-carpelled fruit of *Reseda odorata* L. is seen from above in Fig. 1 A. The top of the ovary is partially closed by four incurved triangular flaps, each of which is formed from the fused margins of two adjacent carpels; the arrows indicate the boundaries between the carpels. Fig. 1, B and C, show external views of the gynaeceum of *R. lutea* L., while Fig. D, a segment cut tangentially from the fruit of *R. luteola* L. and viewed from the inside, indicates the situation of the turn-over flap which occurs above each placenta. Fig. 1, E1–E5, represent transverse sections from a series through the apical region of a gynaeceum of *R. alba*, in which the transmitting tissue (dotted) can be traced from the cavity of the ovary to the stigmas. The midrib regions of the four carpels are lettered A, B, C, D, and their marginal regions, A′, A′; B′, B′; C′, C′; D′, D′. Carpels C and D are cut at a slightly higher level than A and B. The uppermost ovule borne by the placenta marked A′+B′ is seen in Fig. 1, E2. At this level the tip of the corresponding downwardly directed triangular flap projects freely into the ovary cavity, and it is seen to contain a single transmitting canal (dotted). At a slightly lower level (E1) the transmitting tissue in the flap is seen to have reached the actual surface, so that it would