FLORAL ANATOMY IN RELATION TO TAXONOMY*

V. Puri

School of Plant Morphology, Meerut

ABSTRACT

The systematist has to look forward to workers in different disciplines of botany for features and correlations that may be of interest to him in making his classification the "epitome of our knowledge of plants". It has been our endeavour here to indicate the way in which studies in floral anatomy have helped the taxonomist in achieving this object.

Variations in the vascular plan of the flower, as in floral structures, are numerous and they have been classified under the following heads: (1) Reduction, (2) Amplification, (3) Cohesion and (4) Adnation. All these modifications have, in some way or another, helped the taxonomist by providing him additional data.

Some specific examples from Ranunculaceae, Umbelliferae, Polygalaceae, Gentianaceae, Papilionatae, Rutaceae and Apocynaceae are then given to show how floral anatomy has been helpful to the systematist in strengthening or sometimes rejecting his inferences. Besides, it is inferred that floral anatomy may also contributed valuable data in determining correlations in larger groups such as orders.

In conlusion it is pleaded that floral anatomists should make their studies more comprehensive than what they hitherto have been. Besides, they should also realize that, like any other branch of study, floral anatomy also has certain limitations. Ignoring them will be as harmful to the cause of floral anatomy as exaggerating them.

With the simple object that he may make his classification the "epitome of our knowledge of plants" the systematist has to look forward to workers in different disciplines of botany for features and correlations that may be of interest to him. It will be my endeavour here to indicate the way in which studies in floral anatomy have helped the taxonomist in the performance of his arduous task.

The usefulness of the anatomical method is sometimes believed to be due to the so-called 'conservative' nature of vascular bundles. But the recent discussions have emphasized that the doctrine of conservatism of vascular bundles is unsound and no longer tenable. Notwithstanding this the vascular bundles still show some variations that may be useful in determining similarities and correlations between different forms.

Variations in the vascular plan of the flower, as in floral structures are numerous and they may be classified under the following heads: (1) Reduction**, (2) Amplification**, (3) Cohesion** and (4) Adnation**. All these modifications have in some way or the other helped the taxonomist by providing him additional data.

1. Modification through Reduction.—Reduction in the number of vascular bundles in a flower is brought about through definite loss either of organ or of bundles in an organ or through fusion. Occasionally entire whorls of organs, particularly those of petals and stamens may be 'lost' completely.

In such cases the corresponding vascular bundles may also disappear completely. But sometimes the so-called vascular stubs are seen continuing in the receptacle for short distances. These are interpreted as 'trace' parts—those parts which traverse the receptacular cortex as against the 'bundle' parts that traverse the organs—and are generally assumed to show reduction rather than amplification. In the Passifloraceae, for instance, there is typically a single whorl of stamens but anatomical evidence in the form of-vascular stubs, for a second whorl, which is completely lost externally is also available in some species (Puri, 1947). A similar situation has been reported in a number of other families including Polemoniaceae (Dawson, 1936), Cyperaceae (Blaser, 1941), Caricaceae (Devi, 1952) etc.

2. Modification through Amplification.—In some cases floral organs may receive more than the usual number of vascular traces†. Petals in certain species of the Winteraceae (Nast, 1944), Degeneriaceae (Swamy, 1949), Papaveraceae (Dickson, 1935), Cucurbitaceae (Miller, 1929), etc., receive three bundles each instead of the usual one. In the same way stamens in some of the ranalian families may have three traces each and the carpels 5, 7 or even more.

3. Modification through Cohesion.—Cohesion or fusion between parts of the same whorl has perhaps been the most active factor in modifying the ground vascular plan of the flower. This has affected considerably the number of veins in calyx, corolla and gynoecium. The number of ribs in the calyx of certain families, particularly the Caryophyllaceae and Labiatae is an important taxonomic character.

^{*} Research contribution No: 49 from the School of Plant Morphology, Meerut College, Meerut.

^{**} These terms are used in the 'phylogenetic' rather than in 'outogenetic' sense,

[†] This does not refer to several bundles which may be produced by branching of a single bundle in an organ.

In the case of ovary, cohesion has resulted in much greater complexities in the vascular ground plan. Not only do the carpellary ventrals and the median laterals show various stages of fusion in pairs but sometimes the fusion is so "deep-seated" that the two bundles arise as one from the parent stele. In achenial carpels, which are generally believed to be reduced forms of follicle types, the vascular supply has been reduced to the simplest. In Ranunculus aquatilis, for instance, the simple sub-basal ovule appears to be borne on 'dorsal' bundle, this situation having been brought about by complete fusion of ventrals to the dorsal bundle (Chute, 1930).

4. Modification through Adnation.—Vascular bundles of organs of different whorls may fuse together if they happen to occur close to one another radially or tangentially. The commonest example is perhaps that of the sepal marginals which in many cases arise conjoint with petal dorsals. Sometimes two sepal marginals, one petal midrib and one staminal bundle may all arise as a single trace which in the receptacular cortex separates into its component parts. In case of extreme compression even the carpellary dorsals also may arise fused with the sepal-petal-stamen strand. Such cases are often seen in the "wall" of an inferior ovary.

Let us now consider some common examples where vascular anatomy has been helpful to the systematist in strengthening or sometimes rejecting his inferences. Unlike genetical studies which help in determining relationships of smaller groups such as species, vascular anatomy of the flower usually helps in ranking taxa of higher order such as genera and families.

Paeonia.—Recently Eames (1953) has summed up admirably well the systematic position of this genus. Floral anatomy, wood anatomy, embryology*, comparative morphology, cytology, all justify the removal of this genus from the Ranunculaceae and the erection of a new family, Paeoniaceae, for it. In Paeonia sepals and petals receive few to several traces while in other genera of the Ranunculaceae generally sepals get three and petals one trace each. Stamens in Paeonia present a marked contrast to the condition in other genera. They are centrifugal in development and receive traces from conjoint strands which arise from the parent stele (Fig. 1, A.B.) The carpel also is unlike that of other genera both anatomically and histologically. It has 5, 7 or more traces as against three in other genera.

These and some other considerations suggest that *Paeonia* is not even related to the Ranunculaceae. Eames (1953) considers Paeoniaceae to be best placed near Dilleniaceae (Fig. 1, C).

Hydrocotyle asiatica L. (Umbelliferae) has long been separated as Centella asiatica (L.) Urban.

Recently Mittal (1955) has confirmed this on anatomical grounds. He finds the inflorescence in

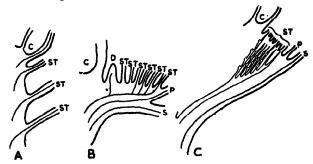


Fig. 1. Diagrams to show vascular supply to stamens of Aquilegia canadensis (A), Paeonia Delavayi (B) and Dillenia indica (C). (After Eames, 1951). C, carpel; D, disc appendage; P, petal; ST, stamen and S, sepal.

Centella to be a cyme and in Hydrocotyle, an 'umbellose raceme'. Besides, the two ovules in Centella receive their vascular supply from alternate bundles in each carpel. In species of Hydrocotyle, on the other hand, ovular traces are derived from placental strands, the fusion product of ventral traces.

Polygalaceae.—Dube (1960), on the basis of a detailed morphological study of the Polygalaceae and allied families in this laboratory has concluded that in the tribe Polygalae the flower is constructed on a hexamerous plan there being six sepals, two petals (4 suppressed) and 8 stamens (4 suppressed). In P. arillata Dube has found evidence for 6 petals and 12 stamens. In addition to the two petals he finds two rudimentary petals and two petals being incorporated in the keel. This last organ according to him is a triple structure of which the median portion is formed of a sepal and the lateral portions of petals, one on either side. He has found interesting evidence for so interpreting the different parts of the keel. In P. amera, for instance, he observes that only the median portions of the keel contains 'pouches' like other sepals, but the lateral portions like other petals lack them completely. Besides, its three traces arise quite independently on different radii.

Dube (1960) further concludes that the genus Polygala is a heterogeneous mixture and needs thorough revision. He is particularly sceptical about Polygala arillata which he suggests to be raised to the status of a distinct genus. It differs from other species in possessing shrubby habit, large handsome flowers, two rudimentary lateral petals and a prominent collar-like intrastaminal disc. Besides, in characters of the anther and of the seeds it occupies a unique position in the genus. While all the other species of Polygala (excepting P. triphylla var. glaucescence) have bisporangiate anthers dehiscing longitudinally, P. arillata has 4-sporangiate anthers dehiscing by tangential slit. Again while other species have albuminous seeds with more or less

^{*} The embryogeny of this genus has been much controverted during recent years, but the opinion now seems to be settled in favour of coenocytic mode of embryo development (See Matthiessen, 1962).

hairs, P. arillata has exalbuminous seeds which are devoid of hairs and almost covered with fleshy red strophiole. Then this is the only species that has been studied which has a keel with three traces arising from three different gaps, in all others they arise from a common gap.

In view of all these considerations, some of which are indeed very weighty, *Polygala arillata* deserves to be separated from the rest of the species of *Polygala*

and be put into a separate genus.

In the same way the species Polygala triphylla and P. triphylla var. glaucescence occupy a unique position in the family in so far as their pollen characters are concerned. While the family is usually characterised by radiosymmetric, isopolar, ellipsoidal and polycolpotate pollen graîns those in P. triphylla and P. triphylla var. glaucescence are bilateral, heteropolar, boat-shaped (cf. monocotyledons) and polycolporate. These are important features not only for the Polygalaceae but also for the dicotyledonous plants for they are usually met with in monocotyledons.

Notwithstanding these common characters Polygala triphylla and P. triphylla var. glaucescence differs markedly from one another in a number of other characters. For instance in P. triphylla the anthers are 2-sporangiate and dehisce by longitudinal slit, the intra-staminal disc is small and non-vascular the median bundle of the keel remains unbranched whereas in P. triphylla var. glaucescence the anthers are 4-sporangiate and dehisce by tangential slit, the intra-staminal disc is produced into two lateral flaps and is vascularized and the median bundle of the keel branches to supply the simple crest of two earlike lobes.

In view of these and several other minor differences of size and shape Dube (1960) has suggested that *P. triphylla* var. *glaucescence* should be raised to the status of a distinct species having some marked affinities with *P. arillata*.

Gentianaceae.—A recent anatomical study of the Gentianaceae (Gopal & Puri, 1962) reveals that the vasculature of the flower in the two sub-families, Gentianoideae and Menyanthoideae is fairly distinctive. In Menyanthoideae it is more specialized in so far as it shows cohesion and adnation of traces supplying different organs. The adjacent ventral carpel bundles and their corresponding half placentae also remain fused completely. In addition, the carpellary traces in Linnanthemum are the first to diverge and indicates a tendency towards epigyny. These are distinctive features of the Menyanthoideae but whether the sub-family should be given the status of an independent family is for the taxonomists to decide.

In the sub-family Gentianoideae the variations in the gynoecium vascular supply are somewhat significant in so far as they show some correlation with the type of placentation. In all members of the Exacinae except Cotylanthera, where the placentation is essentially axile, each carpel receives five traces—one dorsal, two secondary, marginals and two ventrals. In all other sub-tribes studied, the placentation is essentially parietal, and each carpel, as a rule, receives only three traces—one dorsal and two ventrals. It is concluded, therefore, that in the Gentianaceae the five-trace condition is generally characteristic of closed carpels with axile placentation and the three-trace condition, of open carpels with parietal placentation.

Further, in Gentiana and Swertia there is a marked tendency for the two halves of a placenta to separate, so much so that in some cases the four groups of ovules lie equidistant from one another. The fact that within each group all ovules are oriented in the same way clearly indicates that it represents only half of a placenta. It seems necessary to emphasize this point, as in some other cases similarly separated half-placentae have been misinterpreted as full placentae (See Gopal & Puri, 1962).

Papilionatae.—Moore's (1936 a) study of the vascular anatomy of the flower of certain species of the Papilionatae not only sustains the well-established

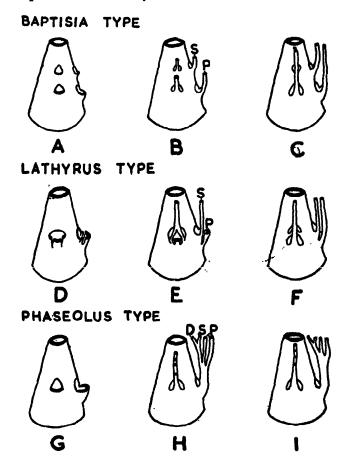


Fig. 2. Diagrams illustrating the salient features of the floral anatomy of Papilionatae. Carpellary traces not shown.

Baptisia type.—Two nodes of petals (P) and stamens
(S) separated by a relatively long internode.

Lathyrus type.—Internode separating corolla and androecium is greatly shortened. Phaseolus type.—Traces to floral appendages on the same radius are fused and depart from stele as one large strand. D, disc trace.

(After Moore, 1936 b).

classification of the family but also brings to notice new characters of great taxonomic importance. Notwithstanding the apparent uniformity in the organization of the papilionaceous flower, the vascular ground plan shows definite and significant trends. Moore distinguishes two anatomical series according to the nodal relationships of the traces to the sepals and petals and to the stamens. These are designated as (1) Dihiate (Hiatus, meaning gap or cleft) series and (2) Unihiate series. In the Dihiate series there are two sets of traces (and gaps) which supply calyx, corolla and stamens. This is further distinguished into (a) Baptisia type and (b) Lathyrus type. All

genera studied by Moore from Sophoreae, Podalyrieae, Genisteae fall under Baptisia type (Fig. 2, A-C) and those from Trifolieae, Loteae, Galegeae, Hedysareae, Dalbergieae and Vicieae under Lathyrus type (fig. 2, D-F). In the Unihiate series, on the other hand, there is one set of gaps from which one set of traces depart which later on split into calyx, corolla and stamen traces (fig. 2, G-I). Under this there is only the Phaseolus type that includes all genera studied in Phaseoleae. This is further characterized by the possession of a staminodal disc—a character which has not been taken advantage of by taxonomists—and climbing habit.

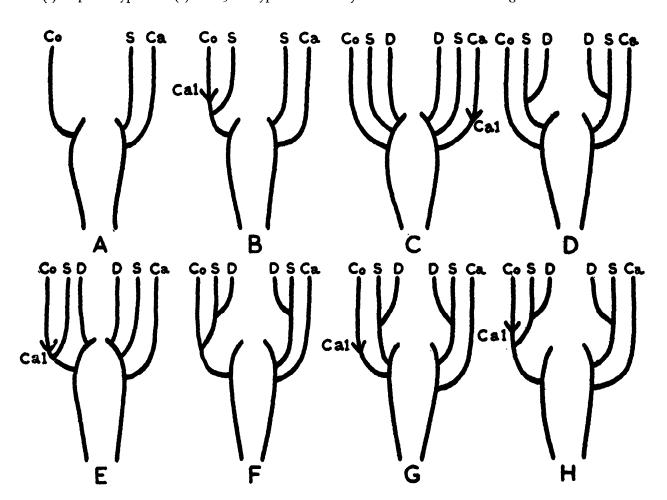


Fig. 3. Diagrams showing the vertical relationships of the vascular traces in the flowers of various Rutaceae. A. In Diosma succulenta, Xanthoxylum fraxineum, Toddalia aculeata, Feronia elephantum, Aegle sepiaria. B. In Cheoridium dumosum. C. In Ruta bracteosa, R. graveolens, Triphasia trifoliata. D. In Ptelea trifoliata, Citrus aurantium.

E. In Adenandra uniflora, Barosma crenulata, Calodendrum capensis. F. In Agathosma imbricata.

G. In Boronia fastigiata, B. heterophylla, B. megastigma. H. In Dictamnus fraxinella.

Ca, calyx trace; Cal, calyx lateral trace; Co, petal trace; D, disc trace;

S, stamen trace. (After Moore, 1936 a).

Rutaceae.—Moore (1936 b), who has analysed Saunders' data on Rutaceae has found eight different sorts of anatomical conditions which differ in (1) adnation of traces, (2) cohesion of traces, (3) insertion of stamen traces and (4) insertion of disc traces (fig. 3, A-H). Type A is believed to be the

simplest and Type H the most complex. The sub-family Rutoideae exhibits seven of the eight types and is, therefore, considered to be most heterogeneous phylogenetically: Ruta and Citrus, which are generally placed rather far apart by systematists, show rather similar floral anatomy

(Type C & D). It is significant to note that Barner's (1927) observations of serodiagnosis agree remarkably well with those of floral anatomy. On the other hand Ruta and Dictamnus, which are placed very near to one another by taxonomists, show different floral anatomy (types C & H). Further information, alone can decide which is the correct treatment.

Floral anatomy has also contributed valuable data in determining correlations in larger groups such as orders. On the basis of his recent studies the present author has reached the conclusion that the gynaeceum make-up in the Papaveraceae, Capparidaceae, Cruciferae and Moringaceae is essentially on the same plan. In all of them, although the placentation is parietal, the placental bundles are inverted with reference to the floral axis and occur on the inner side of the secondary marginal strands with normal orientation. The structural feature, which strengthens considerably the inclusion of the doubtful Moringaceae in the Rhoeadales, has been responsible for the suggestion that parietal placentation in these families is a further modification of axile placentation. And as this peculiarity has also been reported in the Passifloraceae and Cucurbitaceae (Puri, 1947, 1954) it supports the suggested affinities between the Moringaceae and the Passifloraceae.

Then there may be some cases in which anatomical studies may not be of any help from the taxonomic point of view. Having made a comprehensive study Woodson & Moore (1938), for instance, reached the conclusion that in this family the results of a study of vascular anatomy of the flower appear to be of

little value to pure taxonomy.

It is pity that so far the so-called anatomical studies of the flower are essentially confined to studying the course and distribution of vascular bundles within the receptacle and floral organs. Recent work has shown that epidermis and mesophyll characters in the study of foliage leaves have yielded useful taxonomic information. Floral anatomists will do well if they also make their studies more comprehensive than what they hitherto have been. Besides, they should also realize, that, like any other branch of study, floral anatomy also has certain limitations. Ignoring them will be as harmful to their cause as exaggerating them.

ACKNOWLEDGEMENT

I am thankful to Dr. Radhey Shiam for inking the diagrams illustrating this article.

LITERATURE CITED

- Barner, J. Serodiagnostische Verwandschaftforschungen innerhalb der Geranales, Sapindales, Rhamnalesund Malvales. Bibl. bot. Stuttgart, 94: 1-39, 1927.
- Blaser, H. W. Studies in the morphology of Cyperaceae. 1. A & B. Amer. J. Bot. 28: 542-551 and 832-838, 1941.
- Chute, H. M. The morphology and anatomy of the achene. Amer. J. Bot. 17: 703-722, 1930.
- Dawson, M. L. The floral morphology of the Polemoniaceac. Amer. J. Bot. 23: 501-511, 1936.
- Devi, Shanti. Studies in the order Pavietales. III. Vascular anatomy of the flower of Carica papaya L. with special reference to the structure of the gynaeceum. Proc. Indian Acad. Sci. 36B: 59-69, 1952.
- Dickson, Jean. Studies in floral anatomy. II. The floral anatomy of Glaucium flayum with reference to other members of the Papaveraceae. J. Linn. Soc. (Bot.) 50: 175-224, 1935.
- Dube, V. P. Morphological and anatomical studies in Polygalaceae and its allied families. Unpublished Ph. D. Thesis Agra University. 1960.
- DUBE, V. P. Morphological and anatomical studies in Polygalaceae and its Allied families. Unpublished Ph. D. Thesis, Agra University. 1960.
- EAMES, A. J. Floral anatomy as an aid in generic limitation. Chron. Bot. 14: 126-32, 1953,
- GOPAL, K. AND V. PURI. Morphology of the flower of some Gentianaceae with special reference to placentation. Bot. Gaz. 124: 42-57, 1962.
- MATTHIESSEN, A. A contribution to the embryogeny of Paeonia. Acta Horti. Berg. 20: 57-61, 1962.
- MILLER, W. L. Staminate flower of Echinocystis lobata. Bot. Gaz. 88: 262-284, 1929.
- MITTAL, S. P. A contribution to the morphology of Centella asiatica (Linn.) Urban, and some related species. J. Indian bot. Soc. 248-261, 1955.
- MOORE, J. A. The vascular anatomy of the flower in the papilioneceous Leguminosae 1 & 2. Amer. J. Bot. 23: 279-290; 349-355, 1936a.
- ——Floral anatomy and phylogeny in the Rutaceae. New Phytol. 35:318-322, 1936b.
- NAST, C. G. The comparative morphology of the Winteraceae. VI. Vascular anatomy of the flowering shoot. J. Arnold Arb. 25: 454-466, 1944.
- Puri, V. Studies in floral anatomy. IV. Vascular anatomy of the flower of certain species of the Passifloraceae. *Amer. J. Bot.* 34: 562-573, 1947.
- ——Studies in floral anatomy VII. On placentation in the Cucurbitaceae. *Phytomorphology* 4: 278-99, 1954.
- Woodson, R. E. Jr. and J. A. Moore. The vascular anatomy and comparative morphology of apocynaceous flower. Bull. Torrey Bot. Club. 65: 135-166, 1938.
- Swamy, B. G. L. Further contribution to the morphology of the Degeneriaceae. J. Arnold. Arb., 30: 10-38, 1949.