MORPHOLOGY OF THE GYNOECIUM IN LABIATAE

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SUMMARY

Two gynoecial primordia are initiated as discrete units but soon get interconnected by the occurrence of interprimordial growth between them. A rim of meristematic tissue thus produced gives rise to the ovary wall by zonal growth. The residual floral apex grows parallel to the gynoecial primordia in the form of a septum. The two placental ridges arise from the inner lateral walls of the ovary, grow into the ovarian cavity, and ultimately fuse with the axial septum. The anterio- posterior region of the ovary wall also grows into the ovarian cavity to form a false septum which divides each locule into two. The Labiatae show a placentation which is neither true axile nor true parietal but an intermediate condition between the two, as the septum grows like in a typical axile placentation and the placentae like in typical parietal placentation. The gynobase in Labiatae is considered to be carpellary in nature.

INTRODUCTION

The morphology of the gynoecium and the pertinent terminology are eliciting more debate than those regarding any other plant part. A number of concepts dealing with gynoecial diversity have been elaborated (e.g. Saunders, 1925, 1934, 1937-1939; Troll, 1928, 1939b; Thomas, 1935, 1936; Thompson, 1934, 1936; Leinfellner, 1951; Lam, 1959; Eames, 1961; Puri, 1951, 1952, 1961, 1964; Melville, 1961, 1962; Meeuse, 1963, 1966, 1973; Sattler, 1974). The gynoecium in Labiatae exhibits a rather interesting situation due to the presence of the so called gynobasic style and a placentation of disputable nature. In view of the rudimentary state of our knowledge on the development of the gynoecium in the Labiatae, the present investigation has been undertaken to get a better insight into the morphology of the gynoecium.

MATERIALS AND METHODS

Six taxa of Labiatae viz. *Ocimum basilicum* L., *Coleus blumei* Benth., *Pogostemon benghalensis* (Burm. f.) O. Ktze., *Nepeta spicata* Benth., *Salvia splendens* Sello, and *Teucrium quadrifarium* Buch.-Ham. were taken for the present investigation. Inflorescences in various stages of development collected from Meerut and Mussoorie were immediately fixed either in formalinacetic acid-alcohol (FAA) or Carnoy's fluid (3:1 ethanol : glacial acetic acid). The materials for histological examinations were dehydrated in a tertiary butyl alcohol series and embedded in paraffin wax following customary methods. The sections were cut at 5–6 μm and stained in safranin-orange G-tannic acid combination following the schedule outlined by Sharman (1943). Whole immature inflorescences were stained in 1 per cent solution of acid fuschin in 95 per cent ethanol, differentiated in 70 to 90 per cent ethanol, and then dissected and photographed

completely immersed in 100 per cent ethanol to obtain pictures of three dimensional developmental stages (Sattler, 1968).

OBSERVATIONS

By and large there is a sequential development of different whorls of floral appendages i.e. calyx, corolla, androecium and gynoecium. Two crescent shaped gynoecial primordia arise simultaneously in anterio-posterior plane (Plate 1 A, B). Soon after their inception they become interconnected by the occurence of interprimordial growth. The cylindrical portion thus formed gives rise to the ovary (Plate 1 C). The two gynoecial primordia grow vertically, become appressed, and later fuse post-genitally to form style and stigma (Plate 1 D–G). In later stages of ovary development, four regions of the ovary opposite the locules grow rapidly upwards and outwards, the ovary as a consequence becomes four lobed, the style gets deeply sunken in between these lobes and appears to be arising from the base of the gynoecium (Plate 1 G–I).

Following stamen initiation the floral apex undergoes a period of enlargement by divisions in the outer corpus layers. The carpel primordia are initiated at a time when the floral apex is between 75 microns (*Pogostemon benghalensis*) and 105 microns (*Salvia splendens*) in width. The cells of the inner tunica elongate vertically and then divide by periclinal walls. This is followed by periclinal divisions in the cells of outer corpus layers. The divisions in the corpus are, however, mainly responsible for the initial outgrowth of the carpel primordia (Plate 2 A–C).

When the carpel primordia are between 30 and 45 microns high, apical and subapical initials begin to differentiate which mark the onset of the apical meristematic activity (Plate 2 D). The apical initials and their derivatives divide anticlinally forming the carpel protoderm, and the subapical initials divide in anticlinal and oblique planes giving rise to abaxial and adaxial derivatives. The former undergo further periclinal divisions producing abaxial and middle layers, while the adaxial derivatives give rise to the mesophyll. The cells of the middle layer divide longitudinally and their differentiation brings about the formation of the dorsal procambial strand of the carpel (Plate 2D, E). The apical meristematic activity ceases when the carpel primordia are between 100 microns (*Pogostemon benghalensis*) and 150 microns high (*Salvia splendens*). The cessation being evident by enlargement, vacuolation, and light staining reactions of the cells in the apical region of the carpel primordia.

The carpel primordia also undergo a limited amount of marginal growth. The anticlinal and oblique divisions of the submarginal initials produce adaxial and abaxial derivatives which further divide periclinally forming the mesophyll of the carpel. The most extensive marginal growth takes place in the distal region of the carpel.

Due to more extensive growth and cell enlargement in the abaxial region of the carpel than in the adaxial, the primordia become curved in toward each other arching over the remaining floral apex (Plate 2 F). All members studied presently, with the exception of *Nepeta spicata*, exhibit growth in thickness by an adaxial meristem (Plate 2 F, G). The adaxial meristematic activity is first indicated by periclinal divisions in the subprotoderm of the carpel primordium when the latter is between 75–80 microns (*Coleus blumei*) and 100-130 microns (*Salvia splendens* and *Ocimum basilicum*). Continued adaxial meris-

tematic activity causes the ventral surface of the two carpel primordia to expand and come in contact. The adaxial meristem does not extend to the extreme tip of the carpel primordia. The more proximal ventrally extended region represents the style, whereas the distal undilated region of the carpel primordia forms the stigma. The stylar portion of the carpel primordia undergoes ontogenetic fusion by interlocking of the epidermal cells. This interlocking forms a common tissue that by intercalary cell divisions and cell elongation forms the cylindrical style (Plate 2 H). The distal free parts of the carpel primordia form the stigma, and in a transection through the stigmatic region the carpel primordia appear as two free organs in the process of marginal growth. At a lower level they are closely appressed whereas still lower in the stylar region they are fused. In *Nepeta*, where adaxial meristem is not formed, the adaxial margins of the two carpel primordia come in close appression due to hyponastic curvature only, and their epidermal cells get interlocked resulting in ontogenetic fusion (Plate 2 J). This interlocking proceeds acropetally but never reaches the extreme tips of the carpels. The distal free region forms the stigma while the more proximal region where fusion has taken place forms the style (Plate 2 I).

Development of the ovary and ovule initiation:

Early in ontogeny, the two carpel (gynoecial) primordia, which are initiated as discrete units, become connate by the occurence of interprimordial growth between them. An activated cylinder of tissue is thus formed at the base of the gynoecial primordia (Plate 1 B, C). The cells of this region divide by anticlinal oblique walls adding to the vertical growth of the region which forms the ovary wall.

Following inception of the carpel primordia, the summit of the remaining floral apex which still retains a double layered tunica is nearly flat (Plate 2 D, E). But soon the apex assumes a dome shaped appearance due to periclinal and oblique divisions in the cells of the outer corpus layers, and strict anticlinal divisions in the cells of both the tunica layers (Plate 2 F, G). However, in *Ocimum basilicum* the residual floral apex shows a number of periclinal divisions in its second tunica layer also. Due to this extensive meristematic activity the residual floral apex grows up in the form of a septum parallel to the long axis of the carpel primordia (Plate 2 G).

Two placental ridges arise on the lateral ovary walls by periclinal divisions in the subhypodermal layer (Plate 2 H; 4 A). In transectional view the placental ridges appear as two meristematic mounds projecting into the ovarian cavity (Plate 3 A, B; 4 C; 5 A). As the placental ridges grow inward they block most of the ovarian cavity. With the inward extension of the placentae into the ovarian cavity, the vertically growing septum becomes closely appressed with the placental margins (Plate 3 C, D). This is followed by ontogenetic fusion of the cells of the placentae with those of the axial septum through interlocking, and consequently the ovary becomes bilocular (Plate 2 H). The fusion of the placentae with the axial septum produces a homogenous mass of tissue which grows by intercalary cell divisions and cell enlargement (Plate 3 E). As a result, in a longitudinal section, the ovule bearing tissue of the gynoecium appears to be a prolongation of the axis, while actually it is formed by the carpellary tissue only which later on gets fused with the septum (Plate 2 H, I; 5 B).

A transectional series of the ovary of *Salvia splendens*, about 110 microns high, helps in

explaining this peculiar type of development more clearly. At the base the ovary is a solid mass of cells with septal tissue in the centre and two dorsal procambial strands situated in the ground tissue of the ovary in an anterio-posterior plane. The cells of the septum are distinguishable from rest of the tissue by their large nuclei and dense cytoplasm (Plate 4 A). The septum grows to a height of 75 to 80 microns from the base of the ovary. The region from 60 to 75 microns high illustrates the fusion of the two placental ridges with the septum in the centre (Plate 4 B, C). Beyond this region the placental ridges start receding back, and as a result the ovary becomes unilocular (Plate 4 E, E).

Simultaneously with the development of the placentae, the anterio-posterior walls of the ovary also start growing inward by periclinal and oblique divisions in the hypodermal and subhypodermal layers. The two projections thus produced extend inward and get fused with the axial septum. This septum consequently makes the ovary tetralocular (Plate 5 A, B).

The ovule initiation starts immediately after the fusion of axial septum with placental ridges. The placental surface becomes markedly broadened and two ovules are initiated on each placenta (Plate 5 A). Their initiation starts by periclinal divisions in the hypodermal layer. The protoderm of the ovule maintains its distinctness early in ontogeny by consistent anticlinal divisions. A single subprotodermal cell then becomes differentiated in the apical region of the ovule. This cell, which is conspicuous because of its large size, dense cytoplasm, and enlarged nucleus, directly functions as the megasporocyte.

In successive stages of development the ovule continues to elongate and undergoes a typical anatropous curvature. A single integument is initiated by divisions in the protoderm and subprotoderm layers, and it grows down as a collar of tissue around the nucellus (Plate 2 J).

To accommodate the developing ovules, the ovary grows upward and outward in four regions opposite the ovules by divisions in the ovary wall. As a result of this the style is surrounded by the lobes of the ovary and appears to be arising from the base of the ovary (Plate 1 G–I).

Development of the gynobase:

In six taxa of the family investigated the development of the gynobase (disc) varies to a considerable extent. The greatest development of this disc (the region where it appears highest) is between the two adjacent ovules. In *Salvia splendens* and *Coleus blumei* the gynobase is unequally four lobed, the anterior lobe being larger than the rest, and overtopping the overian lobes (Plate 1 G, H). In *Ocimum basilicum, Pogostemon benghalensis* and *Teucrium quadrifarium* the gynobase is not as prominent as in the above two taxa and is uniformly four lobed (Plate 1 I). In *Nepeta spicata* no disc could be observed even in its rudimentary form.

The disc is initiated by periclinal and oblique divisions in the hypodermal layer of the basal region of the ovary wall. The divisions are more frequent in the four regions alternating with the lobes of the ovary, and consequently the disc becomes four lobed. In *Salvia splendens* and *Coleus blumei* the cells in the anterior lobe remain active for a longer duration hence this lobe overtops others. The disc receives its vascular supply from the dorsal procambial strand of the carpel.

Procambial development:

There are two different modes of procambial development in the taxa investigated. In *Ocimum basilicum, Coleus blumei, Pogostemon benghalensis*, and *Nepeta spicata*, soon after the initiation of gynoecial primordia, the procambial cylinder elongates anterio-posteriorly and gives off two procambial strands in the median plane of the carpel primordia. These are the dorsal procambial strands of the carpels. They are followed by two ventral procambial strands. The dorsal and ventral procambial strands lie at different radii and each ventral strand branches into two before innervating the two ovules formed on a placenta. In *Salvia splendens* and *Teucrium quadrifarium* the basal procambial cylinder becomes extended towards the gynoecium. First it gives off two procambial strands in the median plane of the carpels, then it extends gradually toward the placentae and differentiates into four procambial strands. The former are the dorsal and the latter are the ventral procambial strands of the carpels. Here also the dorsal and ventral strands lie at different radii and two ventral strands of a carpel directly innervate the two ovule primordia formed on a placenta.

DISCUSSION

According to the widely accepted classical interpretation of the gynoecium, the basic unit of the gynoecium is 'carpel' which is generally defined as an appendage bearing and enclosing ovule(s) (e.g. Brown, 1840; Van Tieghem, 1871; Henslow, 1891; Eames, 1931, 1951, 1953; Troll, 1939a, b; Douglas, 1944; Wilson and Just, 1939; Joshi, 1947 and Puri, 1951, 1961, 1962, 1964). Croizat (1960, 1962, 1964, 1973) pointed out that in several angiosperms ovule(s) and gynoecial appendage do not form a structural unit, and he, therefore, suggested that 'placenta' and 'gynoecial appendage' are more basic units of gynoecial structure.

Sattler (1974) cited many examples of the gynoecia where placentae and ovules are formed not on the gynoecial primordia but on the floral apex or receptacle or intercalation e.g. *Ochna, Illicium, Myrica, Juglans, Fagopyrum, Stipa, Stylidium, Balanophora, Scyphostegia,* several Cyperaceae and Juncaceae. And, on the basis of these examples he concludes that the concept of 'carpel' can not be universally applied to all angiosperms. He suggests his own conceptual frame work which describes the enormous diversity of gynoecial construction, and proposes the use of terms 'gynoecial primordium', 'gynoecial appendage', 'placenta', 'ovule', and 'megasporangium'. A gynoecial appendage develops from a gynoecial primordium, and is a structure which either forms the whole gynoecium or a part of it except placenta(e) and/or ovule(s).

The development of gynoecium of Labiatae shows that the gynoecial primordia which are directly formed on the floral apex develop into gynoecial appendage. The septum, however, is a direct continuation of the floral apex, but it fuses with the placentae (which bear ovules) formed on the gynoecial appendage.

The gynoecium of Labiatae, as a rule, is bicarpellary and syncarpous with a bilocular ovary which becomes tetralocular at maturity due to intrusion of the anterio-posterior ovary wall (Lawrence, 1951; Hutchinson, 1969; Cronquist, 1968).

The formation of syncarpous gynoecia has been variously interpreted by different workers. According to Leinfellner (1950, 1951) syncarpous gynoecia are formed by

congenital fusion, however, such a fusion is not observable during ontogeny. Payer (1857), on the basis of his study of the organogenesis of flower of *Tupa ignescens*, reported that in this taxon the carpel primordia arise as C-shaped structures, but by the phenomenon of the mergence of growth centres they become united. Kaplan (1968b) also considered the carpel union of *Downingia bacigalupii* similar to that of *Tupa*. According to Cusick (1966) the fusion of growth centres of Payer (1857) is also a sort of ontogenetic fusion but different from the traditional post-genital fusion. According to Hagemann's (1970) notion all sorts of cups and cylindrical structures, etc., are formed by the process of meristematic fusion (special kind of zonal growth) which have traditionally been described as the products of congenital fusion.

In taxa of Labiatae investigated by the present authors two gynoecial primordia are initiated as discrete units on the floral apex. Following their inception interprimordial growth occurs between them and thus an activated cylinder of meristematic tissue is formed which gives rise to the ovary wall by zonal growth. Hence, the formation of the syncarpous gynoecium in Labiatae can be described by the process of post-genital fusion rather than by congenital fusion (c.f. Sattler, 1974).

The free distal region of the gynoecial primordia grow apically for some time, and then gets fused post-genitally by interlocking of the epidermal layers except for at the extreme tips. The more proximal fused region forms the style while the distal one gives rise to the bifid stigma. Such fusion involved in the formation of the style has been reported earlier by several workers (e.g. Baum, 1949; Boke, 1949; Leinfellner, 1951; Tepfer, 1953; Hartl, 1956; Kaplan, 1968b; Singh and Jain, 1975).

After the formation of the gynoecial primordia in Labiatae, the residual floral apex grows upward to form a septum. The two placental ridges arise from the inner lateral ovary walls (fused margins of two carpels) by divisions in the cells of the hypodermal layer. They grow inward into the ovarian cavity, consequently fuse with the vertically growing septum, and thus the ovarian cavity is divided into two locules. The ovules are borne on these placental ridges which arise independently of the septum. Thus the placentae and septum are of different origin. The anterio-posterior region of the ovary wall also grows inward to form a false septum at right angle to the existing septum, and this makes the ovary tetralocular.

The longitudinal sections of the ovary, perpendicular to the septum and the false septum, exhibit different structural details, particularly in older floral buds. The former shows both septum and placentae while the latter shows only the septum. Hence the placentae give an impression to be arising as axial structures.

In taxa with typical axile placentation, the septum grows from what morphologically represents the summit of the floral apex and ultimately gets fused with the carpel walls dividing the ovarian cavity into locules. The placentae which bear ovules are formed by divisions in the cells of the hypodermal layer of the septum. The placental ridges, however, arise from the lateral walls of the ovary in those taxa which exhibit typically parietal placentation. The Labiatae show an intermediate condition between the two described above, that is, the septum develops as in case of typical axile placentation, whereas the placentae arise from the lateral walls of the ovary (fused margins of the two carpels). The septum and placentae have dual nature, the former being axial and the latter appendicular in nature.

The procambial development of the Labiatae shows that the dorsal and ventral procambial strands of the carpels are present on different radii, the latter innervate the ovules belonging to two different carpels. These anatomical criteria are suggestive of parietal placentation (see Puri, 1952).

Hence the Labiatae shows a placentation which is neither true axile nor true parietal, but an intermediate condition between the two. It may be possible that axile placentation is on its way to becoming parietal where axial septum, typical of axile placentation, is still retained, but the placentae grow from the inner wall of the ovary.

In Labiatae the ovary is mounted on a more or less well developed gynobase which is generally four lobed and non-nectariferous (Lawrence, 1951). In six taxa of the family investigated the development of the gynobase (disc) varies to a considerable extent. The greatest development of the disc, and the area where it appears highest, is between the nutlets. In *Salvia splendens* and *Coleus blumei*, the gynobase is unequally four lobed, the anterior lobe being larger than the rest and overtopping the ovarian lobes. In *Ocimum basilicum, Pogostemon benghalensis* and *Teucrium quadrifarium* the gynobase is not as prominent as in the above two taxa and is uniformly four lobed. In *Nepeta spicata* no disc could be observed even in its rudimentary form.

The disc is initiated by periclinal divisions in the hypodermal layer of the basal region of the ovary wall. The divisions are more frequent in the four regions alternating with the four lobes of the ovary, consequently the disc becomes four lobed. A somewhat similar mode of initiation of the disc has been reported in Acanthaceae (Singh and Jain, 1975) and Bignoniaceae (Jain, 1977) where it has been interpreted as carpellary in nature. Hitchcock (1932), too, considered the disc in *Lycium* (Solanaceae) as composed of ovary tissue.

The disc of Labiatae receives its vascular supply from the dorsal procambial strands of the carpels. The vascular supply to the disc is differentiated quite late in the ontogeny of flowers.

Woodson and Moore (1938) consider the nectaries around the ovary as definite appendages and not merely meaningless hypertrophies of the receptacle, as they contain definite vascular tissue associated with that of the gynoecium proper. Hence they interpret the disc lobes surrounding the base of the ovary in Apocynaceae to be carpellodes. When studying the floral anatomy of the Boraginaceae, Lawrence (1937) observed that the dorsal trace is clearly differentiated well below the disc. He, therefore, considers the disc as a part of the ovary formed by an increased proliferation of the swollen bases of the ovary. Moore (1936) studied the morphological nature of the disc in *Martensia* (Boraginaceae) which consists of four unequal lobes, those occuring on the carpel backs being smaller and those alternating with them being equal to or larger than the nutlets. On the basis of the vasculature it was inferred that the smaller members of the gynobase are formed from the basal region of the carpels while the larger ones appear to be simple carpellodes.

The disc surrounding the base of the ovary has been observed in several families of bicarpellatae, e.g. Oleaceae, Boraginaceae, Apocynaceae, Convolvulaceae, Bignoniaceae, Acanthaceae, etc. whereas it is vascular in some and nonvascular in others (Puri and Agarwal, 1976). Rao (1971), who made a detailed study of the disc in several dicotyledonous families, is of the opinion that the disc is an 'organ sui generis' in majority

of cases, receiving its vascular supply from whatever traces are conveniently located.

The ontogeny and procambial supply of the disc in the Labiatae suggest its carpellary nature as it arises from the base of ovary and also receives its procambial supply from the dorsal strand of the carpel.

REFERENCES

BAUM, H. 1949. Über die postgenitale verwachsung in karpellen. Öster. Bot. Z. 95: 86–94.
Boke, N. H. 1949. Development of the stamens and carpels in Vinca rosea L. Am. J. Bot. 36: 535–547.
BROWN, R. 1840. On the relative position of the divisions of stigma and parietal placentae in the compound ovarium of plants. Misc. Bot. Works. Robert Brown 1: 555–563.
CROIZAT, L. 1960. Principa Botanica. Caracas.
—— 1962. Space, Time, Form: The Biological Synthesis. Caracas.
—— 1964. Thoughts on high systematics, phylogeny and floral morphology, with a note on the origin of the angiospermae. Candollea 19: 18–96.
—— 1973. Les Euphorbiacées des vues en elles Mêmes, et dans leurs rapports enver l'angiospermie en général. Mem. Soc. Brot. 23: 1–206.
CRONQUIST, A. 1968. The Evolution and Classification of Flowering Plants. Thomas Nelson & Sons, Ltd., London.
CUSICK, F. 1966. On phylogenetic and ontogenetic fusions. In E. G. Cutler (ed.), Trends in Plant Morphogenesis. pp. 170–183. Longmans Green & Co., Ltd., London.
DOUGLAS, G. E. 1944. The inferior ovary. Bot. Rev. 10: 125–186.
EAMES, A. J. 1931. The vascular anatomy of the flower with refutation of the theory of carpel polymorphism. Am. J. Bot. 18: 147–188.
—— 1951. Again: 'The new morphology'. New Phytol. 50: 17–35.
—— 1953. Floral anatomy as an aid in generic limitation. Chronica Bot. 14: 126-132.
—— 1961. Morphology of the Angiosperms. McGraw-Hill Book Co. Inc., New York.
HAGEMANN, W. 1970. Studien zur Entwicklungsgeschichte der Angiospermenblätter. Bot. Jb. 90: 297-413.
HARTL, D. 1956. Morphologische studien am pistill der scrophulariaceen. Öster. Bot. Z. 103: 185–242.
HENSLOW, G. 1891. On the vascular system of floral organs, and their importance in the interpretation of the morphology of flowers. J. Linn. Soc. Lond. Bot. 28: 151–197.
HITCHCOCK, C. L. 1932. A monographic study of the genus Lycium of the Western hemisphere. Ann. Missouri Bot. Gard. 19: 179–348.
HUTCHINSON, J. 1969. Evolution and Phylogeny of Flowering Plants. Academic Press, Inc. (London) Ltd., London.
JAIN, D. K. 1977. Morphological, Anatomical and Ontogenetic Studies in Bignoniaceae, Ph. D. thesis, Meerut University, Meerut.
JOSHI, A. C. 1947. Floral histogenesis and carpel morphology. J. Indian bot. Soc. 26: 62–74.
KAPLAN, D. R. 1968. Histogenesis of the androecium and gynoecium in Downingia bacigalupii. Am. J. Bot. 55: 933–950.
LAM, H. 1959. Taxonomy, general principles and angiosperms: 3–375. In W. B. Turrill (ed.), Vistas in botany. Vol. 1. London.
LAWRENCE, J. R. 1937. A correlation of the taxonomy and the floral anatomy of certain Boraginaceae. Am. J. Bot. 24: 433-444.
LAWRENCE, G. H. M. 1951. Taxonomy of Vascular Plants. The Mac-Millan Co., New York.
LEINFELLNER, W. 1950. Der Bauplan des synkarpen Gynözeums. Öster. Bot. Z. 97: 403–436.
—— 1951. Die Nachamung der durch kongenitale verwachsung entstandenan Formen des Gynözeums durch postgenitale Verschmelzungsvorgänge. Öster. Bot. Z. 98: 403-411.
MELVILLE, R. 1961. A new theory of the angiosperm flower. Nature (Lond.) 188: 14–18.
—— 1962: A new theory of the angiosperm flower: 1. The gynoecium. Kew Bull. 16: 1–50.
MEEUSE, A. D. J. 1963. From ovule to ovary: a contribution to the phylogeny of the megasporangium. Acta biotheor. 16: 127–182.
—— 1966. Fundamentals of Phytomorphology. The Ronald Press, New York.
—— 1973. Some fundamental principles in interpretative floral morphology. In T. M. Varghese & R. K. Grover (eds.), Vistas in Plant Sciences. Vol. I. International Biosciences Publications, Hissar.

MOORE, J. M. 1936. Morphology of the gynobase in Mertensia. Am. Mid. Nat. 17: 749–752.

PAYER, J. B. 1857. Traité d'organogénic comparee de la fleur. Librairie de Victor Masson, Paris.

PURI, V. 1951. The role of floral anatomy in the solution of morphological problems. Bot. Rev. 17: 471–553.

—— 1952. Placentation in Angiosperms. Bot. Rev. 18: 603–651.

—— 1961. The classical concept of angiosperm carpel: A reassessment. J. Indian bot. Soc. 40: 511–524.

—— 1962. On the concept of carpellary margins. In P. Maheshwari et al. (eds.) Proceedings of the Summer School in Botany, Darjeeling, pp. 326–333. Ministry of SR and CA, Govt. of India, New Delhi.

—— 1964. On the relation between ovule and carpel. J. Indian bot. Soc. 42: 189–198.

—— and R. M. AGARWAL. 1976. On accessary floral organs. J. Indian bot. Soc. 55: 95–114.

RAO, V. S. 1971. The disc and its vasculature in the flowers of some dicotyledons. Bot. Notiser 124: 442–450.

SATTLER, R. 1968. A technique for the study of floral development. Can. J. Bot. 46: 720–722.

—— 1974. A new approach to gynoecial morphology. Phytomorphology 24: 22–34.

SAUNDERS, E. R. 1925. On carpel polymorphism. I. Ann. Bot. (Lond.) 39: 123–167.

—— 1934. Comments on floral anatomy and its morphological interpretations. New Phytol. 33: 127–170.

—— 1937–1939. Floral morphology: A New Outlook with Special Reference to the Interpretation of the Gynoecium. W. Heffer & Sons Ltd., Cambridge.

SINGH, V. and D. K. JAIN. 1975. Floral development of Justicia gendarussa (Acanthaceae). Bot. J. Linn. Soc. 70: 243–253.

TEPFER, S. S. 1953. Floral anatomy and ontogeny in Aquilegia formosa var. truncata and Ranunculus repens. Univ. Calif. Publ. Bot. 25: 513–648.

THOMAS, H. H. 1935. On the concepts of plant morphology with special reference to view and comments on the nature of the angiospermic stigma. New Phytol. 34: 113–121.

—— 1936. Palaeobotany and the origin of Angiosperms Bot. Rev. 2: 397–418.

THOMPSON, H. M. 1934. Comments on recent statements regarding the nature and origin of the angiospermic stigma. New Phytol. 33: 306-315.

THOMPSON, J. M. 1936. Ontogeny of the angiospermic carpel. Nature (Lond.) 137: 458–459.

TROLL, W. 1928. Zur auffassung des parakarpen gynaeceums and des coenokarpen gynaeceums Uberhampt. Planta. 6: 255–276.

—— 1939a. Vergleichende Morphologie der höheren Pflanzen. Bd. 1 Vegetation sorgane. Teil 2. Gebruder Borntraeger, Berlin.

—— 1939b. Die morphologische Nature der karpelle. Chron. Bot. 5: 38–41.

*VAN TIEGHEM P. H. 1871. Recherches sur la structure du pistil et sus l'anatomi Comparée de la fleur. Mem Savanets etrangess a l'Inst. 21: 1–261.

WILSON, C. L. and T. JUST. 1939. The morphology of the flower. Bot. Rev. 5: 97–131.

WOODSON, R. E. and J. A. MOORE. 1938. The vascular anatomy and comparative morphology of apocynaceous flowers. Bull. Torrey bot. Club. 65: 135–166.

EXPLANATION OF PLATES

PLATE I A–I. × 80

A. A floral bud of *Nepeta spicata* in top view after initiation of sepal (K), petal (C), and stamen (A) primordia.

B. A floral bud of *Coleus blumei* in top view at the time of inception of gynoecial primordia (G). Sepal primordia were removed to exhibit inner floral appendages.

C. A floral bud of *Coleus blumei* in top view where sepals and petals were removed to exhibit the developing gynoecial primordia (G).

D. A comparatively older floral bud of *Salvia spelendens* where sepal and petal primordia were removed to exhibit gynoecial primordia. Stamen (A) and staminodes (S) are also visible on outer side of the gynoecial primordia (G).

E, F. Gynoecia of floral buds of *Ocimum basilicum* showing differentiation into ovary (O), Style (SY) and Stigma (ST).

* Not seen in original.

G. Gynoecium of a floral bud of *Salvia splendens* at a still later stage of development.
H. Gynoecium of a floral bud of *Salvia splendens* in top view where style was removed (rSY) to exhibit four lobes of ovary (OV) and the disc (D) with its much developed anterior lobe.
I. Gynoecium of a floral bud of *Ocimum basilium* where style was removed (rSY) to exhibit four lobes of ovary (OV) and an equally four lobed disc (D).

PLATE II

A. Longitudinal section of a floral bud of *Coleus blumei* before initiation of carpel primordia × 280.
B. Longitudinal section of a floral bud of *Teucrium quadrifarium* during the initiation of carpel primordia (G). Note periclinal divisions in the second tunica layer. × 280.
C. Longitudinal section of a floral bud of *Ocimum basilicum*, showing very young carpel primordia. × 280.
D. E. Longitudinal sections of floral buds of *Coleus blumei* and *Teucrium quadrifarium* respectively, exhibiting apical meristematic activity in carpel primordia. D × 430; E × 280.
F. Longitudinal section of a floral bud of *Ocimum basilicum* cut perpendicular to the septum, showing the growth of residual floral apex (F). × 280.
G. Longitudinal section of a floral bud of *Coleus blumei*, cut perpendicular to the septum showing growth of the residual floral apex into septum (SM). Adaxial meristematic activity is also visible near the carpel tips. × 280.
H. A part of longitudinal section of the gynoecium of *Salvia splendens* cut perpendicular to the septum, showing the two locules formed by fusion of septal and carpellary tissue. × 400.
I. Longitudinal section of gynoecium of *Nepeta spicata* cut perpendicular to the septum, showing ovule primordia (O). × 280.
J. A part of transection of a floral bud of *Ocimum basilicum* through the ovarian region, showing an ovule primordium with a single integument (IN) surrounding the central nucellus (N). × 220.

PLATE III

A, B. Longitudinal sections of the gynoecium of *Ocimum basilicum* cut perpendicular to the false septum, showing septum (SM) and the placentae (P). × 310.
C, D. Longitudinal sections of the gynoecium of *Ocimum basilicum*, cut perpendicular to the false septum, showing fusion of the septum with the placentae. C × 120; D × 140.
E. Longitudinal section of a gynoecium of *Ocimum basilicum* after fusion of septum with the placentae showing the ovule primordia × 120.

PLATE IV. A–E × 240

A–E. A transectional series through an ovary of *Salvia splendens* about 110 microns high from below upward exhibiting fusion of the septum (SM) with the placental ridges (P) in figures B and C, and receding back of the placentae in figures D and E.

PLATE V

A. Transection of an ovary of *Ocimum basilicum*, showing two placental ridges. Note the inward growth of the anterio-posterior ovary wall in the form of false septum. × 340.
B. Transection of an ovary of *Salvia splendens* showing development of ovules (O) on the placental ridges (P). The false septum (FSM) is showing fusion with the axial septum making the ovary tetralocular. × 120.

Abbreviations used:
   AL - Anther lobe; A - Stamen primordium; C - Petal primordium; Co - Connective; D - Dorsal procambial strand of the carpel; DI - Disc; F - Floral apex; FSM - False septum; G - Gynoecial primordium; IN - Integument; K - Sepal primordium; N - Nucellus; O - Ovule primordium; OV - Ovary; P - Placenta; rSY - Style removed; S - Staminode; SM - Septum; ST - Stigma; SY - Style; V - Ventral procambial strand of the carpel.
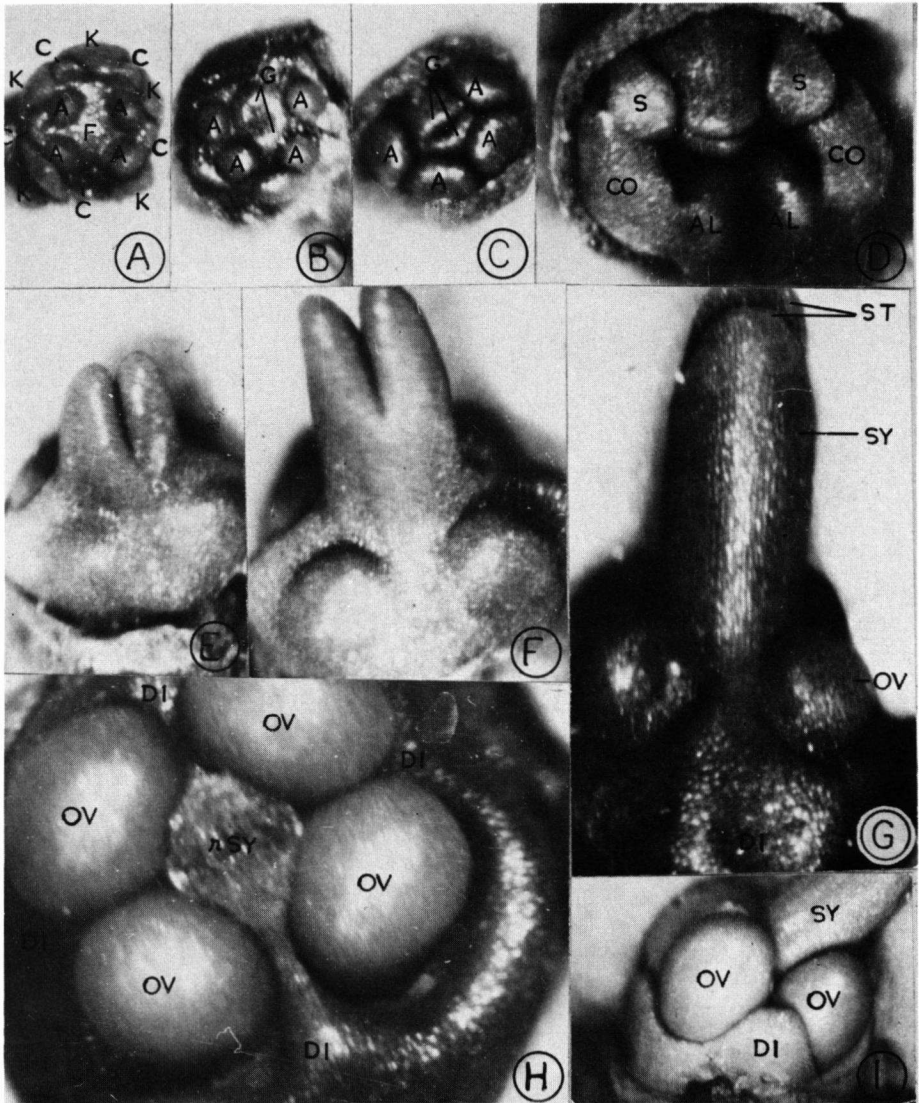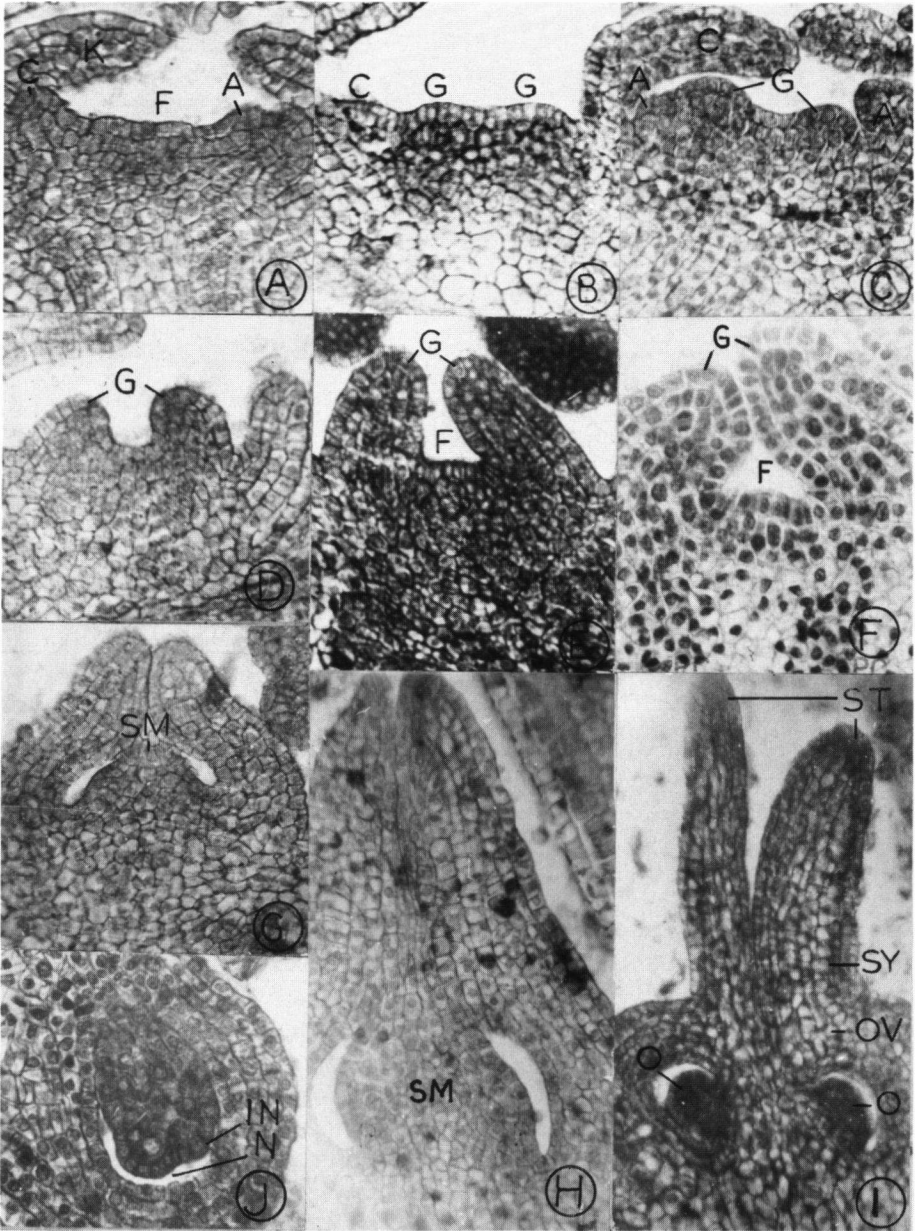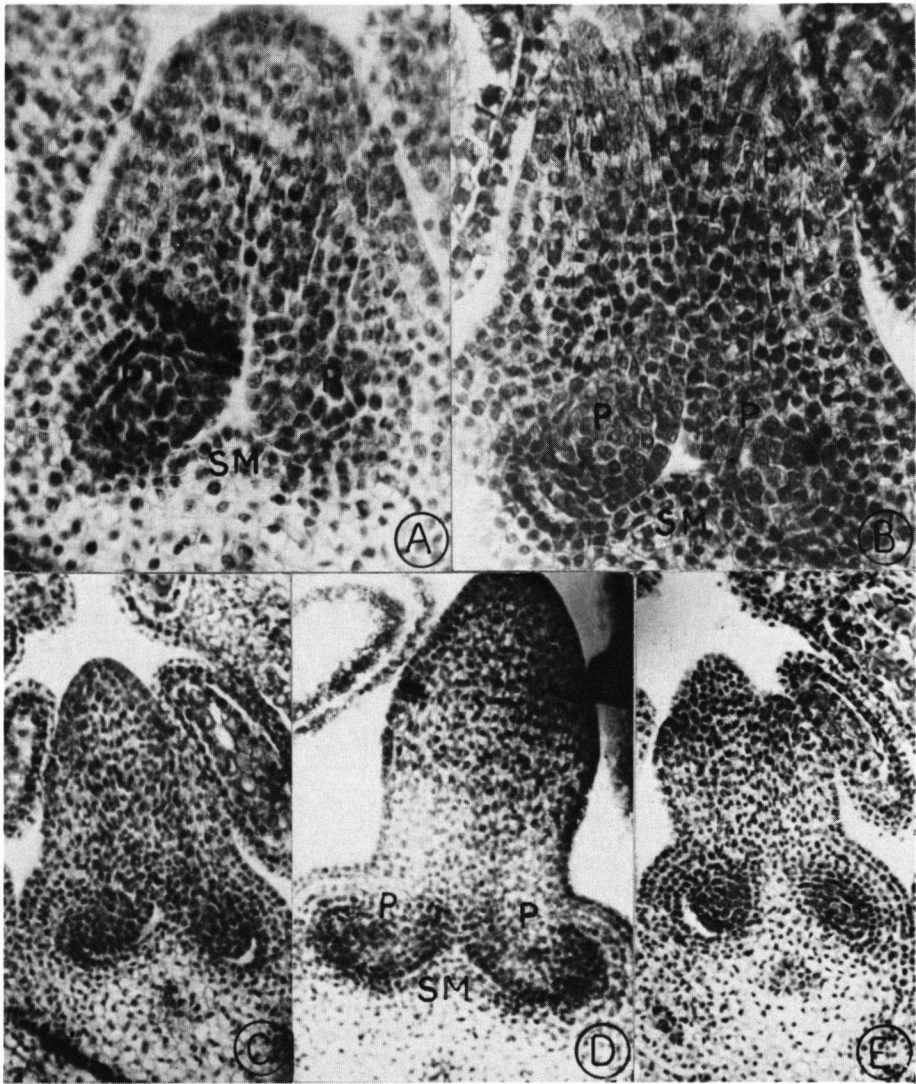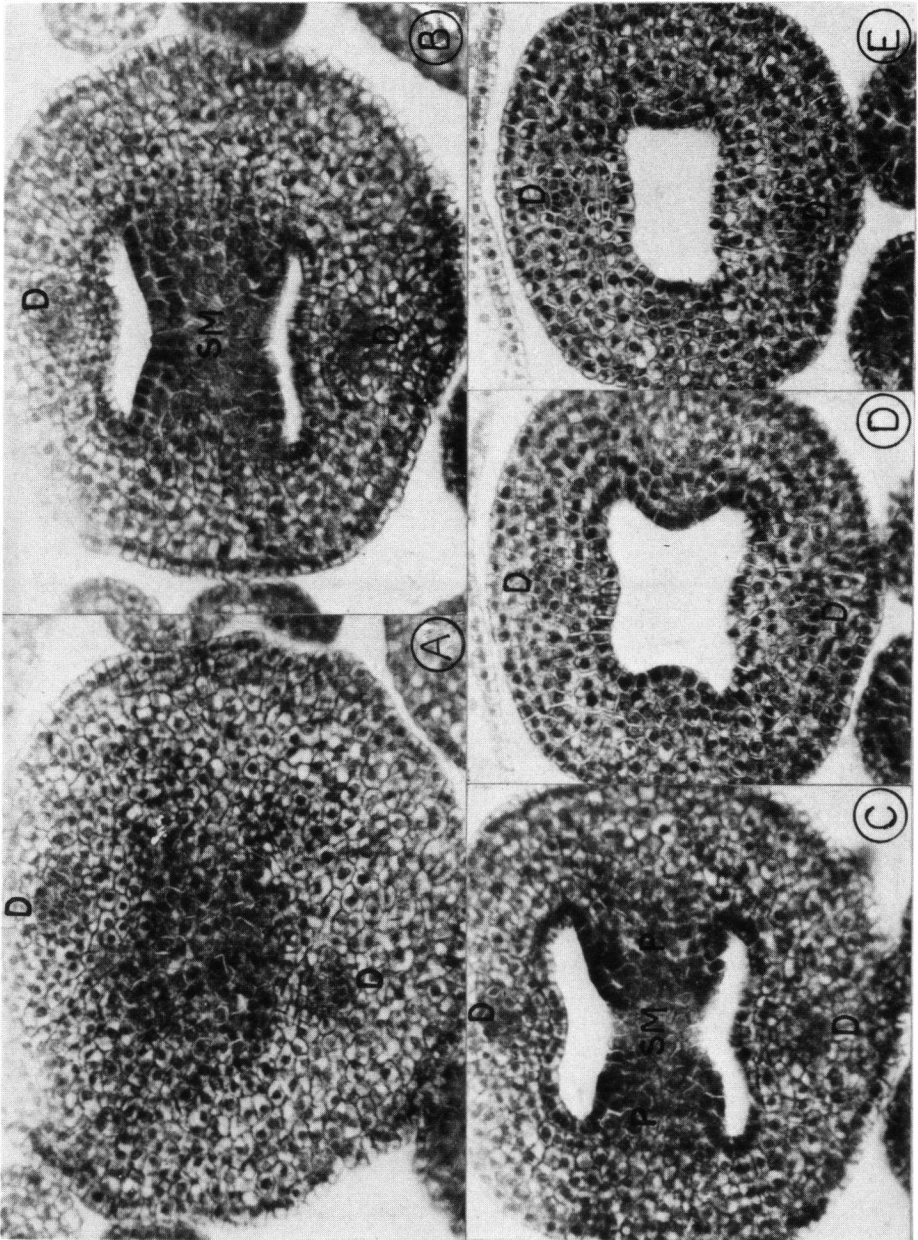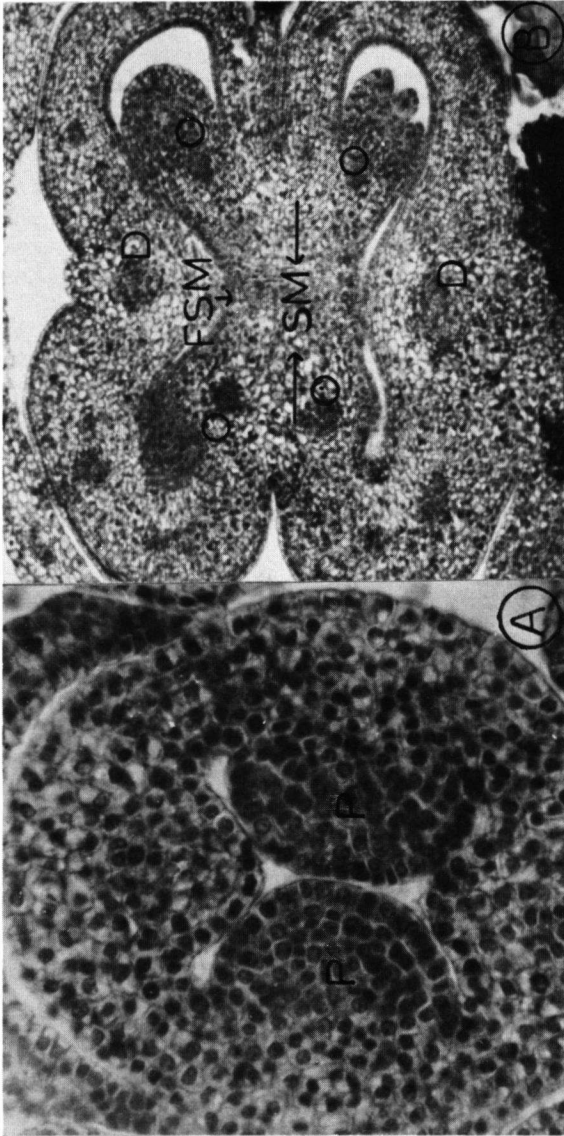
PLATE I

PLATE II

PLATE III

PLATE IV.

PLATE V