FLORAL MORPHOGENESIS OF *BOUGAINVILLEA SPECTABILIS* WILLD., *BOERHAAVIA DIFFUSA* L. AND *MIRABILIS JALAPA* L. (NYCTAGINACEAE)

by

© Louise R. Perlin

A Thesis Re-submitted to the
Faculty of Graduate Studies and Research
in Partial Fulfillment of the Requirements for the
Degree of Master of Science

Department of Biology
McGill University
Montreal, Canada

November 1980

ABSTRACT

The development of the flower and its epiphyllous position on the floral bract of *Bougainvillea spectabilis* Willd. are examined. Floral development in *Bougainvillea* is compared with that of *Boerhaavia diffusa* L. and *Mirabilis jalapa* L. The development of the perianth of all three species is very similar. The five stamens of *Mirabilis* are initiated simultaneously, alternate to the petals, while the eight stamens of *Bougainvillea* arise sequentially at divergence angles suggestive of a 3/8 spiral arrangement. The two stamens of *Boerhaavia* are initiated most frequently towards opposite sides of the floral apex. In all three species, growth occurs in a zone at the periphery of the floral apex to produce the gynoecial wall. The ovule develops in a basal and terminal position and is formed from the gradual upgrowth and transformation of the floral apex. Each flower of *Bougainvillea* is initiated in the axil of a young floral bract. Thereafter, growth occurs at the base of the floral bract and extends into the region where the floral bud is situated. This intercalary growth, evidenced by longitudinal files of cells results in the epiphyllous condition. Previous studies and interpretations of epiphylly and the basal ovule are reviewed and the present data are discussed with reference to these various interpretations.

RESUME

Le développement de la fleur et son emplacement épiphylle sur la bractée florale de Bougainvillea spectabilis Willd. a été observé. Le développement floral de Bougainvillea est comparé a celui de Boerhaavia diffusa L. et Mirabilis jalapa L. Le développement du périanth était semblable pour les trois espèces. Les cinq étamines de Mirabilis apparaissent simultanément s'alternant aux pétales, tandis que les huit étamines de Bougainvillea apparaissent séquentiellement à angles divergents suggérant un arrangement en spirale de 3/8. Les deux étamines de Boerhaavia apparaissent plus fréquemment vers les côtés apposés de l'apex floral. Pour les trois espèces, la croissance se fait dans un zone à la périphérie de l'apex floral pour former la paroi du gynécée. L'ovule se développe à la base, en position terminale et est formée par la croissance graduelle et la transformation de l'apex floral. Chaque fleur de Bougainvillea apparait dans l'aisselle d'une jeune bractée florale. Par la suite, la croissance se fait à la base de la bractée florale et se continue dans la région où se trouve le bourgeon de la fleur. Cette croissance intercalaire, rendue évidente par des files longitudinales de cellules, résulte en une condition épiphylle. Des études et interprétations précédentes sur l'épiphyllie et l'ovule de base sont revues, et les données présentes discutées par rapport à ces différentes interprétations.

ACKNOWLEDGEMENTS

I would like to acknowledge my supervisor, Professor R. Sattler, both for providing me with my initial interest in this area of biology, and for his patience and support throughout its preparation.

I should also like to acknowledge my lab colleagues: M.S.M. Lieu, Claire Cooney-Sovetts, and Emile Daniel, for hours of fruitful discussion as well as companionship during all phases of this study.

Many thanks to Robert Lamarche and his assistants, Guy l'Heureux and the late Paul Gauthier, who contributed by teaching me a great deal about photography and then assisted me with the photographic aspects of this thesis.

Merci to Bernadette Jacquaz for translating the abstract and Helen Rousseau for typing this manuscript.

Finally, I would sincerely like to thank my parents, Dr. and Mrs. A.S. Perlin for their encouragement - particularly during the writing of this thesis.

TABLE OF CONTENTS

INTRODUCTION

In 1790 the poet and philosopher J.W. von Goethe published his comparative work entitled "Versuch die Metamorphose der Pflanzen zu erklären". Herein Goethe presents the view that all lateral appendages belonging to a shoot are foliar in character and distinct from the other fundamental unit of shoot construction - namely, the stem. Goethe therefore believed floral organs to be metamorphosed 'leaves' which have taken up different functions, though he did recognize that compared with the vegetative shoot, the flower is an abbreviated axis without internodes. That there is a common basic scheme underlying both leafy shoot and reproductive organs was a view which was also held by A.P. de Candolle (1813) who wrote: "La transition des organes de la végétation a ceux de la floraison se trouve ainsi graduée, que plus on l'étude, plus on arrive à comprendre cette unité de composition qui fait la base de l'organographie philosophique". These two basic precepts then, that stem and leaf are mutually exclusive categories, and that the 'leaf' is the structural unit of floral organs, form the basis of the classical theory of the shoot, and the classical (or foliar) theory of the Angiosperm flower respectively.

Though both these theories are still well accepted and widely supported in botanical publications, they have not reached the present devoid of criticism.

Since its introduction, the classical theory of the flower especially has undergone a great deal of debate, inspiring many authors in recent decades to suggest alternative interpretations. These include Lam's (1950) view of stachyosporous and phyllosporous flowers, the gonophyll theory (Melville, 1962), Croizat's (1960: Ia) strobilar concept, Meeuse's (1966) anthocorm theory, and his more recent (1973) spurious floral axis concept.

However, no aspect of this theory has been so hotly debated, nor produced such a proliferation of literature as that of the angiosperm 'carpel', a term Lorch (1963:271) states was first introduced by Dunal in 1817, and which classically has been defined as a leafy structure, adaxially folded on its midrib and bearing ovules on its margin. The problems arising from this concept lie in the use of the term 'carpel' for interpreting flowers when it is not clear whether ovules are in fact borne on 'carpel' tissue or on a portion of the floral apex. Such a problem is encountered most notably in flowers with inferior ovaries, and in members of families with either free central or basal placentation. Reviews of the inferior ovary (Douglas, 1944; Puri, 1952) and free central placentation (Moeliono, 1970), as well as a critical study of the various interpretations of gynoecial morphology (Lorch, 1963) have already been undertaken. Therefore, I have restricted the following survey to works which are more directly concerned with my own research on the terminal ovule of several members of the Nyctaginaceae.

In 1931 Grégoire published his dissenting views to the classical floral theory in which he asserted that there is not the slightest morphological connection between vegetative shoot and flower. He carried this further by postulating that the gynoecium differs from the vegetative leaf in being a truly terminal organ. Since Grégoire's time, many botanists have gone to great lengths to interpret their findings on terminal gynoecia and ovules within the framework of the classical theory.

Klaus (1966) looked at the development of Hordeum (Gramineae) and described the terminal ovule in terms of Troll's (1939) peltate theory. This theory accepts the occurrence of terminal gynoecia, but likens the gynoecium to a peltate leaf, the cross zone (Querzone) of which is 'congenitally fused' with the floral apex. Thus, the ovule, initiated on the cross zone would histogenetically still be an integral part of the gynoecium.

A great many morphologists do not accept the existence of terminal organs and are of the opinion that all floral organs are, without exception, initiated on the caulome as lateral 'phyllomes' (Wilson & Just, 1939; Parkin, 1955; Eames, 1961). Parkin (1955:50) wrote: "On a posteriori grounds there is a considerable body of evidence to show that when such organs appear in the adult stage as terminal, ontogeny reveals them as laterally borne in development". The evidence that Parkin cites is vascular anatomy. These workers ascribe to the theory that vasculature is more conservative than external morphology, and that the pattern of primary vascular tissue would reveal the true lateral position of gynoecia and ovules which appear to be terminal. From a study of the vascular system of Hillaria latifolia and Phytolacca acinosa, as well as several other genera of the Phytolocaceae, Eckardt (1954) described the gynoecium (and ovule) in these species as laterally placed. According to him, the placental bundle is not a direct continuation of the axis because an S-shaped curve is made before it enters the ovule. Sharma (1963b:161) looked at several species of the Nyctaginaceae and stated: "A large vascular arc continues up from the receptacular stele and organizing into a large amphicribal bundle, enters the ovule with a sideways bend". Sharma presented this pattern of vascularization as evidence that the single ovule in this family is not terminal. Not all researchers have interpreted results of vascular studies in terms of the classical theory. Earlier, Bhargava (1952) documented a similar bend in the vascular supply to the ovule of Boerhaavia, another member of the Nyctaginaceae. However, he did not regard this as a significant feature, and stated that the ovule was terminal.

There have been a large number of studies in which researchers, looking at terminal ovules, have categorized them as such. As early as 1857 Payer wrote (page 733): "Tout carpelle se compose d'une feuille modifiée et d'un axe qui se bifurque pour porter des ovules". Thus, contrary to the classical floral theory, Payer considered the ovules of all

Angiosperm flowers as stem rather than leaf-borne. Many of the more recent authors who reject the classical concept of the 'carpel' either completely or partly base this rejection and subsequent new interpretations on various hypotheses regarding the phylogeny of the Angiosperms. Most notable perhaps is Lam's (1950) division of the Angiosperms into stachyosporous (cauline or axis-borne) and phyllosporous (carpellary or foliar) families. Several such phylogenetically oriented workers would then interpret a gynoecium with a terminal ovule as composed of a sterile portion called a stegophyll (Lam, 1950), a tegophyll (Melville, 1962), a sterile bract (Meeuse, 1966), or simply a phyllome (Moeliono, 1970), and separate from this, a fertile part consisting of the floral axis with its terminal ovule. For example, Moeliono (1970) carried out histogenetic analyses of various developmental stages of Phytolacca and Hillaria which Eckardt (1954) had previously studied. He rejects Eckardt's view that the single ovule is carpellary and instead asserts that these genera do indeed exhibit terminal ovules. Other researchers who carried out ontogenetic studies on different members of the Gramineae have found that in Oryzopsis (Mehlenbacher, 1970; Maze et al., 1971; Kam, 1974), Anthoxanthum (Sharman, 1960), and Stipa (Maze et al., 1971, 1972), after initiation of the gynoecial wall, the residual apex of the floral primordium increases in size and develops into the ovule. A similar conclusion was reached by Barnard (1957a, 1957b, 1958) working on various genera of the Gramineae, Cyperaceae, and

Juncaceae, by Sattler (1973) who looked at *Fagopyrum*, by MacDonald and Sattler (1973) investigating *Myrica gale*, and by MacDonald (1974) who extended his studies to include *Laportea*. In conjunction with these studies, Sattler (1974a) has proposed the use of a set of terminology which is applicable to the whole range of gynoecial construction, and would therefore also include gynoecia with terminal ovules.

Though the classical shoot theory has not illicited as voluminous or consistent an outpouring of literature as that seen for the foliar theory of the Angiosperm flower, several alternative interpretations of the shoot have been suggested (see, e.g.; Arber, 1950; Lam, 1959; Zimmermann, 1965; Sattler, 1974b). Classically, the shoot theory has stressed strict delimitations between the lateral appendages (phyllomes or 'leaves') and the stem (caulome) portion of a shoot. In addition, this theory would postulate branches arising from the caulome in the axil of a phyllome. However, structures intermediate between caulome and phyllome, such as the cladodes of *Ruscus* (McLean *et al*., 1951) and the phyllomorphs of *Streptocarpus* (Jong, 1970), or the epiphyllous placement of organs or organ systems on a leaf and not in an axillary position on the caulome, do not fit within the confines of the classical theory.

A very extensive review of all varieties of epiphylly - epiphyllous inflorescences and flowers, branches, leaf-like structures, and attached as well as deciduous propagules - has been undertaken by Dickinson (1978). Therefore, I will again restrict the following survey to examples which are most relevant to my own study of the epiphyllous flowers of *Bougainvillea*.

There are a large variety of genera which include epiphyllous species, and the interpretations of them are almost as numerous. Responding to Goethe's earlier observations on the epiphyllous inflorescences of *Tilia* and fertile phylloclades of *Ruscus*, A.P. de Candolle (1827), in keeping with the classical shoot theory, proposed a 'congenital fusion' between fertile and sterile portions of these structures. That is: he postulated that these inflorescences were originally inserted in an axillary position, and had gradually become adnate with their respective subtending leaves during phylogeny. This view has been supported by Planchon (1853), who described inflorescences departing from the lower surface of the leaf in *Erythrochiton hypophyllanthum*. The existence of congenital fusion has also been popularized by several workers such as Moseley (1967) who felt that certain vascular patterns are indicative of fusion having occurred 'congenitally', or during phylogeny. Therefore, Prance (1972), in discussing the vascular anatomy of epiphyllous species of *Dichapetalum*, pointed to the separate leaf and floral traces below the insertion of the inflorescence as evidence of congenital fusion.

However, C. de Candolle (1890), looking at the mature vascular anatomy of epiphyllous inflorescences of *Phyllonoma*, *Helwingia*, and two species of *Polycardia*, was not inclined to interpret his findings within the framework of congenital fusion, and instead described these three species as being leaf products. Earlier, Duchartre (1886) had come to the same conclusions regarding the epiphyllous branches and inflorescences of Begonia ameliae, though he felt that other epiphyllous inflorescences such as those of Helwingia and Phyllonoma did in fact result from congenital fusion.

Bugnon (1958) rejects the notion of congenital fusion entirely and attributes the epiphyllous condition to intercalary growth occurring beneath the primordia of adjacent leaf and inflorescence.

There are also workers who have completely different views of epiphylly. For example, Arber (1950), in setting down her partial shoot theory, states that while most leaves have a reduced ability to give rise to other shoots, there are exceptions. She cites the epiphyllous appendages of cabbage, tomato, Kalanchoe (now Bryophyllum), and Nymphaea as examples of partial shoots with an 'inherent urge' towards the development of whole shoot characteristics.

Another very novel view of epiphylly is that held by Melville (1962). Melville postulates a leaf and its epiphyllous branch as the model of all Angiosperms - flowering as well as vegetative. His study of the epiphyllous inflorescences of Tilia, Phyllonoma, Polycardia, and Helwingia led him to the conclusion that these 'gonophyll' structures have been retained throughout the evolution of these plants.

Most recently, Dickinson and Sattler (1974,1975) looked at the ontogeny of Phyllonoma and Helwingia and found two distinct patterns of growth responsible for the mature epiphyllous positions. In Helwingia the inflorescence is initiated at the base of the leaf primordium. Eventually, basal intercalary growth below the insertion of inflorescence and leaf primordium produces an epiphyllous inflorescence. However, in Phyllonoma, the inflorescence is initiated directly on the adaxial surface of the developing leaf. These studies have contributed toward Sattler's (1974b) new model of the shoot - a scheme which is applicable to the whole range of morphological diversity, and includes epiphyllous structures which previously did not fit into the classical model.

From the above survey, it can be seen that there are wide discrepancies in interpretation of both the terminal ovule, and the epiphyllous condition. Perhaps figuring most prominently in these differing interpretations is the question of whether an author has given priority to the observations made, or to one or another of a variety of philosophical concepts.

The genus Bougainvillea of the Nyctaginaceae is a prime example of a plant which historically researchers have had great difficulty interpreting in terms of both the classical shoot and classical foliar theories. That is: the epiphyllous placement of flower on floral bract, and the single basal ovule found in mature specimens of Bougainvillea are both features which have been subject to all the controversies mentioned on the preceding pages. In addition, the Nyctaginaceae is a family with polymerous androecia. Therefore, workers looking at the comparative vascular anatomy of several genera have postulated an ancestral androecium composed of two staminal whorls for this family, with gradual repression of one of the whorls (Joshi and Rao, 1934; Sharma, 1963b).

Research into the mechanism of growth and development of cases such as Bougainvillea have been of interest to Dr. Sattler and his students for several years. The set of observations reported here from ontogenetic studies of Bougainvillea spectabilis, Mirabilis jalapa, and Boerhaavia diffusa, should, together with previous observations, help clarify current hypotheses, as well as contribute towards an interpretation which is consistent with the observed facts.

MATERIALS AND METHODS

Young shoot tips and inflorescences of *Bougainvillea spectabilis* Willd. at all stages of development, were collected from the greenhouses of Macdonald College Campus, McGill University, and preserved in FAA. Due to the large number of cultivars of *Bougainvillea*, the identity of these specimens was checked following Gillis' (1976) key. Varying floral stages of *Mirabilis jalapa* L. were obtained from the McGill University Greenhouse and preserved in FAA. Voucher specimens of the material studied have been deposited in the McGill University Herbarium, at Macdonald College, Ste. Anne de Bellevue, Quebec. Inflorescences of *Boerhaavia diffusa* L. were collected for me by Ms. S.M. Lieu from the Fairchild Tropical Gardens, Florida, and preserved in FAA. A pressed specimen of this species may be found in the Herbarium of the research laboratory of the above mentioned garden.

Inflorescence apices of all three species were dissected, stained in alcoholic acid fuchsin, and photographed entirely immersed in 100% ethyl alcohol following the technique of Sattler (1968).

Vegetative apices and floral buds of *Bougainvillea* to be sectioned, were dehydrated in a tertiary butyl alcohol series, and infiltrated and embedded in Tissuemat (Fisher), m.p. 61°C. Material was cut at 6-7μ m on a microtome. Sections were stained in Delafield's Hematoxylin with aqueous safranin as a counterstain (Jong, 1970) and photographed using a Zeiss photomicroscope.

Clearings of vegetative leaves and flowers of <u>Bougainvillea</u> were prepared using a Papain NaOH chloral hydrate treatment according to Rodin and Davis (1967). Unstained clearings were photographed with Carl Zeiss luminar macro lenses under incident lighting.

Divergence angle measurements between successive tepal and stamen primordia were made on the uppermost flower of inflorescences at varying developmental stages. These flowers were dissected and photographed from a top view according to Sattler's (1968) technique. Angle measurements were made between the centres of successive primordia using photographic prints of these floral buds which were all enlarged X228.

RESULTS

A. Bougainvillea spectabilis Willd.

I. Morphology of the Node

The foliage leaves are alternate in 2/5 phyllotaxy. In each axil is situated an indeterminate axillary bud, and adaxially to this bud is located the determinate inflorescence axis. Hackett and Sachs (1968) report that when conditions are not favorable for flowering, a typical thorn develops in this position. However, when flowering does occur, the pattern is that of a compound dichasium (Fig. I).

II. Inflorescence Development

An inflorescence is characterized by units of three small flowers - each flower being situated epiphyllously on the upper surface of a bright pink or red showy bract (Figs. I,II). The whole inflorescence is subtended by two inflorescence bracts. In very young developmental stages these two bracts almost completely enclose the inflorescence apex. However, they remain very small, and in the mature form are quite inconspicuous and often fall off.

Shortly after the initiation of the inflorescence apex, the first and then second inflorescence bracts are initiated on either side of it (Plate IA). As the apex enlarges, three flower bract primordia arise in quick succession around its periphery (Plate IB). These bracts then begin to grow, maintaining a slight size difference between them according to their developmental sequence.

As the bracts enlarge, a floral apex is initiated in the axil of each (Plate IC,ID). These floral apices do not arise simultaneously, but are initiated one at a time acropetally. However, their development is in the opposite direction of their initiation, i.e. the upper flower which is initiated last develops faster than the middle and lower flowers which are initiated earlier (Plate IE).

III. Development of the Epiphyllous Condition

As was noted above, a floral apex is borne at the base of the adaxial surface of each of three floral bracts (Plate IC,ID). Initially, the floral bract enlarges due to meristematic activity throughout the entire lamina (Plate IIA). However, as the floral apex enlarges and undergoes perianth initiation, the cells in the abaxial region of the bract enlarge and become more vacuolated than those of the floral apex or adaxial portion of the bract. Therefore, the young bract arches over the floral apex (Plate IIB). During these stages, the floral apex remains situated at the base of the floral bract (Plate IA,IB). However, with the inception of the stamen primordia, and the vacuolation of the abaxial surface of the bract, basal growth begins beneath the insertion of the floral bud in the axil of the floral bract (Plate IIC). This growth appears to proceed principally by cell division and enlargement which is confined to the area between where the floral bract and bud are joined, and the area where the vascular traces to these organs merge. The result is the formation of an intercalated zone of homogeneous tissue evidenced by longitudinal files of cells (Plate IID), and thus the eventual situation of the mature flower in the centre of the floral bract (Plate IIE, Fig. I).

Clearings indicate that there are two sets of vascular traces from the inflorescence peduncle. One set branches continually to supply the length of the bract lamina, while the second set enters the flower and branches repeatedly to supply the various floral organs (Plate IIE).

IV. Floral Development

A. The Flower as a Whole

The mature flower is composed of five perianth members, eight stamens, and one gynoecium containing a single ovule (Fig. IIC). The floral organs are initiated in centripetal succession - the tepals and stamens of each flower arising in either a clockwise or a counter-clockwise direction (compare Plate IIID with Plate IIIE). In a study of the uppermost flower of 155 inflorescences, it was found that about half the flowers (74) exhibited clockwise initiation, while the floral organs of the other half (70) developed in a counter-clockwise direction. Where the uppermost flower of an inflorescence showed clockwise initiation, the floral organs of the second flower developed in a counter-clockwise direction; while the lowermost flower on the inflorescence peduncle again exhibited clockwise initiation. The converse occurred when the uppermost flower was counter-clockwise.

B. Perianth Development

The first two tepal primordia are initiated almost simultaneously, at an average angle of 144°, on the side of the floral apex away from its subtending floral bract (Plate IIIA). Shortly thereafter, the third and then fourth tepal primordia arise at average angles of 141° and 147° respectively from the previously initiated tepal primordium (Plate IIIB). When the third and fourth perianth members are just visible, growth begins to occur in a ring between all the tepals (Plate IIIC) to form a perianth tube which, in the mature condition, encloses the other floral organs. The inception of the last primordium occurs directly on the perianth tube at an average divergence angle of 138° from the fourth tepal member (Plate IIIC).

C. Androecial Development

When all perianth members are readily visible but still very young developmentally, androecial initiation begins. The first two stamen primordia develop in quick succession. In most buds studied, the first stamen primordium is initiated almost opposite perianth lobe one (Plate IIIC). However, several cases were noted in which the inception of this first stamen instead occurred alternate to tepals one and three. Thereafter, a gradual positional shift took place, so that in all the mature floral stages viewed, the first primordium was situated directly (or nearly directly) opposite tepal one. The second stamen primordium then arises alternate to perianth lobes two and four (Plate IIIC, IIID), while the third is quickly initiated alternate to tepals three and five (Plate IIID). When the first three stamen primordia have enlarged slightly, the fourth stamen arises alternate to tepals four and one (Plate IIIE), while the fifth is initiated soon thereafter alternate to tepals five and two (Plate IIIF). A short period of time ensues during which the first five stamen primordia enlarge. At this point the sixth stamen primordium is discernible alternate to perianth lobes one and three (Plate IVA), and the seventh stamen is initiated opposite tepal lobe four (Plate IVB). After considerable development of the previous seven androecial primordia, the inception of the last stamen occurs opposite tepal five (Plate IVC).

Generally little deviation from the above developmental sequence was observed. In two mature flowers, a full complement of only seven stamens was found. But there was no evidence to indicate either initiation or development of more than eight stamens.

Divergence angle measurements were obtained for successive perianth and stamen primordia (Table I). Though there was some variation, perhaps due in part to imprecision in the angle measurement techniques (see Materials and Methods), the results are suggestive of a 2/5 divergence angle in the perianth, with a gradual changeover to a 3/8 spiral arrangement in the androecium.

D. Gynoecial Development

The young floral apex is organized into a two-layered tunica and a corpus (Plate VA). Tepal and stamen primordia arise as small centres of growth on the periphery of the somewhat flattened apex (Plate VB,VC). At the stage where all stamen primordia are distinctly visible, the floral apex becomes dome-shaped (Plate IVC,VC,VD). Thereafter, growth occurs in a semi-circular zone around the periphery of the floral apex, thus producing the gynoecial wall (Plate IVD, Plate VIA-D). After the gynoecial wall has elongated somewhat, an ovule develops in the centre of the gynoecial cavity (Plate VIE-H). The ovule arises in a terminal and basal position and is formed from the gradual upgrowth and transformation of the floral apex. The changeover from the floral apex to the ovule is so gradual that one cannot decide at which stage one should refer to the floral apex as the young ovule primordium. The ovule primordium also retains the tunica-corpus organization of the floral apex (Plate VIH).

As the ovule enlarges two integuments develop centrifugally. These integuments begin by growth on one side of the ovule (that side which is closest to the gynoecial opening) and eventually they completely encircle the young nucellus (Plate VIIB). During its growth the ovule becomes curved (Plate VIIC,D), until at maturity it is of the campylotropous type with the micropyle bent away from the gynoecial opening.

The gynoecial cavity is closed longitudinally by the surface fusion of its lengthwise margins (Plate VIIA). In addition, the dorsal side of the gynoecial wall grows upwards to form a short style and a long hairy stigma. Clearings indicate that a short vascular bundle enters the ovule ventrally, while a long dorsal bundle supplies the gynoecial wall - both traces lignifying basipetally (Plate VIIE,F).

V. Leaf Development as Compared with Epiphylly

The shoot is organized into a two-layered tunica and a corpus, of which the outermost cell layer may resemble a third tunica layer (Plate VIIIA,B). Leaf primordia arise as centres of growth on the periphery of the apical dome in a 2/5 phyllotactic sequence. Initially, each leaf enlarges due to meristematic activity throughout the entire leaf primordium (Plate VIIIA). At a slightly later stage, however, the cells in the abaxial portion of the primordium become larger and increasingly more vacuolated than those of the vegetative apex or the adaxial region of the developing leaf, so that the young leaf arches over the shoot apex. In addition, during this stage an axillary bud is initiated in the leaf axil (Plate VIIIB). Throughout the later stages of leaf growth, the cells in the adaxial portion of the leaf undergo enlargement and vacuolation along with cells in the abaxial region (Plate VIIIC,D).

Unlike the situation previously described for the development of the epiphyllous condition, there is no evidence of an intercalary meristem (or its derivatives) extending across the base of the leaf to the region of the axillary bud. In addition, the vegetative leaf is already quite well developed when axillary bud initiation takes place. This may again be contrasted with floral development where the floral bud is initiated in the axil of a very young totally meristematic floral bract.

B. *Boerhaavia diffusa* L.

I. Vegetative and Floral Morphology

Boerhaavia diffusa is a small perennial herb with decumbent stems and opposite unequal leaves (Fig. IIIA). The small congested head-like inflorescences, borne in the axils of the foliage leaves, are each subtended by two bracts. An inflorescence is characteristically composed of five minute pedicellate flowers, each of which is subtended by one floral bract. In addition, the four outermost flowers of each group bear two smaller sterile floral bracts on their pedicels.

The mature flower is composed of five perianth members, two (or sometimes one or three) stamens, and one gynoecium containing a single ovule (Fig. IIIB,C). Perianth and gynoecial development are described below. In both cases the development is similar to that previously described for *Bougainvillea*.

II. Floral Development

A. Perianth Development

The first and second tepal primordia arise in quick succession at opposite ends of the floral apex (Plate IXA,B). While they enlarge slightly growth occurs in between them around the periphery of the floral apex (Plate IXB), so that the third, and then fourth perianth members appear to be initiated directly on this young perianth tube (Plate IXC). After a short period of time, the last tepal primordium is initiated, again apparently on the perianth tube, in between perianth lobes two and three (Plate IXD).

The above developmental sequence may occur in either a clockwise or counter-clockwise direction as was found in Bougainvillea (compare Plate IXD with Plate IXE). The perianth tube then grows upwards until in the mature flower it completely encloses the other floral organs.

B. Androecial Development

With the inception of the fifth tepal (or, in some cases, slightly before its inception), androecial initiation begins. The first stamen primordium arises opposite perianth lobe one (Plate IXC). Very shortly thereafter, the second stamen primordium is initiated - in some cases alternate to tepals two and four, as was found in Bougainvillea (Plate IXD); but in most buds studied, alternate to tepals two and five (Plate IXE).

In addition to this variation in position of inception, there was also quite a variation in the number of stamens initiated. While most young buds and mature flowers exhibited the standard number of two stamens in the positions described above, a significant number of specimens contained either one or three stamens arising in varying positions on the floral apex (Plate XD,E). There were, however, no cases of staminal numbers larger than three.

C. Gynoecial Development

When the stamens have enlarged substantially, the floral apex becomes dome-shaped (Plate IXF). Thereafter, growth occurs in a semi-circular zone around the periphery of the apex producing a three-sided cylindrical cavity with the gynoecial opening most often facing away from the two stamens (Plate XA,B). However, variations with respect to the gynoecial opening, such as that viewed in Plate XF, were noted. A single ovule primordium is formed terminally in the centre of this gynoecial cavity as was described for Bougainvillea (Plate XA). The gynoecial wall is then closed longitudinally by the surface fusion of its margins (Plate XC). The dorsal side of the gynoecium grows up to form a long filiform style and a stigma.

C. Mirabilis jalapa L.

I. Vegetative and Floral Morphology

Mirabilis jalapa L., a perennial herb with opposite leaves, is native to tropical America and widely acclimatized in Europe as an ornamental. The bright showy inflorescences borne in the axils of the vegetative leaves, each bear two bracts (Fig. IVA). Like *Bougainvillea* the inflorescence is a typical compound dichasial cyme. A comprehensive study of inflorescence initiation and development has been carried out by Wibaut (1965).

The mature flower of *Mirabilis* is composed of five sepals, five petals, five stamens, and one gynoecium containing a single ovule (Fig. IVB,C). It should be noted that the terms 'sepal' and 'petal' are used here in a purely descriptive sense. Based on Heimerl's first comparative study of several genera of the Nyctaginaceae in "Die natürlichen Pflanzenfamilien" (1889), authors of the present day compare one flower of *Mirabilis* with the whole inflorescence of related genera such as *Bougainvillea*, *Boerhaavia*, and *Pisonia*. Thus, the pentamerous 'calyx' of *Mirabilis* is homologized to an involucre which surrounds the one remaining central flower of an originally five-membered inflorescence - all the lateral flowers having been lost through reduction. Similarly, the pentamerous 'corolla' of *Mirabilis* is homologized to the previously described tubular perianth of such flowers as *Bougainvillea* and *Boerhaavia*. For the purposes of this study, however, the correspondingly descriptive terms 'sepal' and 'petal' will be employed.

The floral organs of *Mirabilis* arise in centripetal succession.

II. Floral Development

A. Calyx Development

Shortly after the inception of the floral apex, calyx initiation begins. The first sepal primordium is initiated and develops substantially (Plate XIA), before the second sepal primordium arises towards the other end of the floral apex (Plate XIA). Almost immediately thereafter, the third and fourth sepal primordia are initiated on either side of sepal lobe one (Plate XIB). The final sepal primordium then arises in between sepals one and three (Plate XIC). As was described above for the perianth tubes of Bougainvillea and Boerhaavia, the sepals of Mirabilis may arise in either a clockwise or counter-clockwise direction (compare Plate XIB with Plate XIC). The five sepal primordia continue to grow - sepals one and three at a faster rate than the others (Plate XIC), until they enclose the developing floral apex.

B. Corolla Development

When the five sepals have enlarged, five petal primordia are initiated simultaneously in alternation with the sepals (Plate XIC,D). Almost immediately, growth begins to occur in a ring between the young petal primordia (Plate XID), to produce a corolla tube which in the mature condition completely encloses the other floral organs. Therefore, it can be seen that while the end result is comparable to the perianth tubes of Bougainvillea and Boerhaavia, the plastochron differs.

C. Androecial Development

Androecial initiation begins soon after the young corolla tube becomes distinctive. All five stamen primordia are initiated simultaneously, and arise in alternation with the petal primordia (Plate XIE, Plate XIIA). Of the three species under investigation, Mirabilis showed the least variation with respect to the androecium. In all dissections of mature flowers, five stamens were found. Also, in the younger buds, there was no evidence to indicate either initiation or development of more or less than five androecial primordia.

D. Gynoecial Development

When the five stamen primordia are all distinctly visible, the floral apex becomes dome-shaped (Plate XIIB). Further development is as was previously described for Bougainvillea and Boerhaavia: growth occurs in a semi-circular zone around the periphery of the floral apex to produce a three-sided cylindrical cavity (Plate XIIC,D). A single ovule primordium then arises terminally in the centre of the gynoecial cavity (Plate XIIC). The gynoecial wall is closed longitudinally by the surface fusion of its lengthwise margins. The dorsal side of the gynoecium grows upward to form a very long style and a short capitate stigma.

DISCUSSION

Aside from numerous cytogenetic and horticultural studies, particularly concerning the ornamental varieties of *Bougainvillea* and *Mirabilis*, work on the Nyctaginaceae has not been prolific.

Heimerl (1889), in Engler and Prantl's "Die Natürlichen Pflanzenfamilien", described in great detail and with much precision, the morphology of all genera of the Nyctaginaceae - among them *Bougainvillea*, *Mirabilis*, and *Boerhaavia*. Maheshwari (1929,1930) looked at the anatomy and ontogeny of *Boerhaavia diffusa* with emphasis on mega- and microsporogenesis, while Bhargava (1932) repeated the study on *Boerhaavia repanda* and also looked at stem and leaf anatomy of this species. Cooper (1932) carried out a developmental study of the flower of *Bougainvillea glabra*, and as in the previous works on this family, he paid particular attention to mega- and microsporogenesis. The paper by Joshi and Rao (1934) marks the use of a new methodology in research concerning the Nyctaginaceae. These workers compared the mature floral vascular anatomy of four species - *Boerhaavia diffusa*, B. *repanda*, *Mirabilis jalapa*, and *Bougainvillea spectabilis* - with a view to establishing the phylogenetic affinities of this family. Sharma (1963a) described the vascular anatomy of the node and inflorescence of the same four species which Joshi and Rao (1934) had previously looked at. In a second communication, Sharma (1963b) repeated the earlier studies of floral vascular anatomy and also included a look at two other members of the Nyctaginaceae - *Pisonia linearibracteata* and P. *aculeata*. In a break with the more traditional vasculature research, Wibaut (1965) carried out a very thorough developmental study of *Mirabilis jalapa*, from cotyledon through to and including, the early stages of transition to inflorescence production. More recently, Rohweder and Huber (1974) described the morphology of *Bougainvillea*, *Oxybaphus*, and *Mirabilis*, as well as the ontogeny of the gynoecium of *Mirabilis jalapa*.

Several of the above-mentioned studies have focused on the single perianth whorl and polymerous androecium of various genera of the Nyctaginaceae in relation to other families within the Centrospermales. As early as 1929, Maheshwari, in his developmental study of *Boerhaavia diffusa*, postulated that perhaps a second perianth whorl arose which did not develop fully. He was looking for, but did not find, the missing tepal whorl on its way to elimination. In comparative vasculature studies of several genera, both Joshi and Rao (1934), and Sharma (1963b) described a single set of vascular traces to the perianth of some genera and two sets of alternating traces - one arising at a slightly higher level than the other, to the perianth of other genera. Based on this evidence, Joshi and Rao (1934:181) postulated that "In the family Nyctaginaceae, the two sets of traces for the perianth in the earlier and more primitive condition, and the absence of the upper set and the presence of only one set, is a recent and derived condition." Based on these vasculature findings, there are two possible interpretations which can be made regarding the perianth of the Nyctaginaceae. One theory is that each set of traces originally belonged to a separate whorl. The traces of the lower set supplied the sepals while those of the upper set diverged towards the petals. That the two sets of bundles which still occur in some genera now run in one whorl, would then be interpreted as due to the gradual disappearance of one set of tepal members. The second postulate which has predominated among comparative vascular anatomists (see e.g., Joshi and Rao, 1934; Sharma, 1963b), is that there has always been only one set of tepals in this family. Such workers hold that the primitive number of vascular traces in both a vegetative leaf and a sepal is three, and therefore the ten traces in the Nyctaginaceae are the result of fusion of the laterals of five adjacent tepals. Thus, the lower traces would be regarded as midrib bundles, and the uppers as fused laterals of the five perianth 'leaves'.

Joshi and Rao (1934), in their studies of vascular anatomy, have stated that the perianth portion of the flower shows the greatest variation in vascular supply as compared with the other floral parts of the genera investigated. However, this was not found to be true when developmental stages of these same genera were looked at. Besides the differing plastochron in the corolla of *Mirabilis*, where the petals of this flower are initiated simultaneously, while the calyx of *Mirabilis* and perianth of *Bougainvillea* and *Boerhaavia* are all initiated in a 2/5 spiral sequence, the growth of the tepals in all these genera was remarkably similar and invariable. In addition, there was no evidence in any of the flowers studied that an extra perianth whorl was initiated. Therefore, developmental studies clearly emphasize the presence of only one tepal set in the Nyctaginaceae, with the possible exception of *Mirabilis*.

With respect to the Angiosperms, a great deal has been made of the fact that one typically finds an isomerous condition in the floral organs, or a heteromerous condition in which floral organs are generally in multiples of four or five. Therefore, the polymerous androecia of the Nyctaginaceae, have been the subject of much speculation. Joshi and Rao (1934) asserted that the small number of stamens (1-4), seen in the two species of *Boerhaavia* has been derived by reduction from a higher number such as is seen in *Mirabilis* or *Bougainvillea*. In addition, these workers postulate that perhaps two whorls of five members each was the original condition in *Bougainvillea spectabilis*, with a reduction in one whorl from five to three. A look at mature vascular anatomy convinced Joshi and Rao (1934:180) that two staminal whorls were indeed present:"The outer whorl is of five stamens and is therefore complete. The inner, however, is incomplete and consists only of three stamens." Sharma (1963b) reported that seven to eight stamen traces of *Bougainvillea glabra* arise in groups alternating with the perianth dorsals - two to three traces among these arising singly, the remaining ones in pairs. Therefore, he wrote (pg.160): "It appears that the two staminal whorls considered by Joshi and Rao (1934) as the original condition for the family, have come to occur together in Bougainvillea glabra as a first step toward complete suppression of one of the whorls."

Developmental studies yield a slightly more complex picture than that which has been based on mature vascular anatomy. The stamens of Mirabilis are initiated simultaneously in one whorl alternate with the tepals. However, the stamens of Bougainvillea arise sequentially - some opposite to and others alternate with the tepals. Except in two cases for which the sample size was small, divergence angle measurements between successive stamen primordia were $135^{\circ} \pm 5^{\circ}$. Therefore, both the sequence of primordia development, as well as the angle between these primordia are suggestive of a 3/8 spiral arrangement in the androecium of Bougainvillea. In this flower, the axis on which the stamen primordia arise is so reduced that these stamens come to occur together on one level. Rohweder and Huber (1974) also ascribe a 3/8 spiral to the androecium of Bougainvillea glabra, instead of additional stamens intercalated into a pentamerous cycle. In addition, they question whether isomery is indeed a necessary postulate, and instead feel that the oligomerous nature of Bougainvillea may be related to a change in phyllotaxy from 2/5 to 3/8. The initiation of stamen primordia in Boerhaavia is similar to that which was described for Bougainvillea. However, only two, or occasionally three stamens arise and develop.

While one may postulate, based on mature vascular anatomy, that the polymerous androecia of the Nyctaginaceae are the result of phylogenetic reduction, it is also possible that the stamens of these genera arise in accordance with van Iterson's (1907) speculations. He interpreted the phyllotaxy of any particular species in terms of the relative size of the young primordia and apex, and expanded the idea that the development of primordia on an apex may be regarded as equivalent to a system of touching circles. That is, in terms of size relationships, only certain 'contact systems' are possible. In critical experiments M. and R. Snow (1948) furnished evidence that the next primordium to be initiated originates in the 'first available space' on the apical meristem - the position of the new primordium being determined by the immediate adjacent older primordium. Thus, the androecia of the Nyctaginaceae may be initiated in accordance with this 'most available space' theory. Of van Iterson's theory, Wardlaw (1968) states: "'An available space' of itself does not do anything; rather it is a necessary sustaining condition; it provides a locus in which important morphological development may take place."

One aspect of the Nyctaginaceae which has illicited a great deal of interest over the years is the single basal ovule - a characteristic feature of this family. At the centre of all controversy regarding genera with basal ovules is the classical concept of the Angiosperm 'carpel'. This concept regards the gynoecium, along with all other floral organs as foliar in character, with the ovule or ovules being borne on the margins of the leaf-like 'carpel'. However, in families such as the Nyctaginaceae, there has been a conflict between authors who view the placenta and ovule as an integral part of the 'carpel', and those who believe that the ovule develops independently of the gynoecial wall and is instead a part of the floral axis.

Bound intimately with the classical 'carpel concept' has been the use, by various authors, of anatomical arguments derived from venation pattern and orientation of vascular strands to 'prove' the foliar nature of all gynoecia. One of the first studies of this type was undertaken by van Tieghem (1875) in an attempt to interpret the free central placentation of several Primulaceous gynoecia. Since van Tieghem's time, many workers have become adherents of this theory which postulates that vascular changes lag behind alterations in external morphology and may therefore reveal the true nature of the structure in question - the theory of 'vascular conservatism'. For example, Sharma (1963b:161) found that in all four species of the Nyctaginaceae with which he was working - Boerhaavia diffusa, B. repanda, Mirabilis jalapa, and Bougainvillea spectabilis - "a large vascular arc continues up from the receptacular stele and organizing into a large amphicribal bundle enters the ovule with a sideways bend. This clearly shows that the single ovule in this family is not a terminal structure." Sharma also postulates that the small, blindly-ending xylem elements given out by the ovular bundle towards the centre of the ovule in *Boerhaavia diffusa* are "...obviously the 'residual' axial supply." These two pieces of evidence, in addition to the fact that "the ovule in mature flowers of *Mirabilis jalapa* is not exactly basally borne but occurs slightly to one side of the median line", led Sharma to suggest that the single ovule is the only surviving member of an originally marginal placentation. He, therefore, describes the placentation of this family as sub-basal, according to Puri's (1952) original classification.

A second postulate which has also been used to recover the carpel concept in families such as the Nyctaginaceae with basal ovules, is that of congenital fusion. Thus, Rohweder and Huber (1974), in ontogenetic studies of the gynoecium of *Mirabilis jalapa*, homologize the gynoecium to a peltate leaf: the cross zone (Querzone) of which would be congenitally fused with the floral apex. These workers state that marginal bulges then develop on this peltate protuberance, the median portion of which differentiates into an ovule. Based on this interpretation, which was also put forth by Eckardt (1954) for the Phytolaccaceae, and by Rohweder (1967) for uniovulate members of the Ranunculaceae, these workers maintain that the ovular position is ontogenetically, clearly marginal.

The above two interpretations, however, are contrary to that of Maheshwari (1929:*Boerhaavia diffusa*), Bhargava (1932:*Boerhaavia repanda*), Cooper (1932:*Bougainvillea glabra*), and Joshi and Rao (1934:*Boerhaavia diffusa*, B. *repanda*, *Mirabilis jalapa*, *Bougainvillea spectabilis*). On the grounds of their observations, all these workers considered the ovule of the Nyctaginaceae to be cauline, i.e. a continuation of the floral axis. Pankow (1962), examined the histogenesis of the gynoecium of Mirabilis jalapa. He described the ovule as arising from the floral residual apex and therefore stated that the ovule of this genus is not carpellary. More recently, Moeliono (1970) looked again at Mirabilis, and also restudied Eckardt's (1954) earlier work on several genera of the Phytolaccaceae. Based on these histogenetic and ontogenetic studies, Moeliono felt confident that the ovule in all these species was terminal.

The results of my own studies on three uniovulate genera of the Nyctaginaceae lead me to concur with this latter group of workers. The ovules in Bougainvillea spectabilis, Boerhaavia diffusa, and Mirabilis jalapa are all basal and terminal organs. During development, the floral apex is gradually transformed into an ovule, such as has recently been reported by Kam (1974) for several genera of the Gramineae. In addition, clearings of mature flowers of Bougainvillea do not exhibit a prominent sideways bend in the ovular trace as was described by Sharma (1963b).

Thus the data of the present study do not support a carpellary interpretation of the gynoecium. To apply the carpel concept to the basal ovule of the Nyctaginaceae, one would have to postulate congenital fusion of a cross zone of the carpel with the floral apex, and large modifications in vasculature. Since congenital fusion is nonobservable during ontogeny, it would seem unnecessary to apply such a concept when a descriptive set of data, based on an observable phenomenon, is available.

Curiously enough, besides work carried out by Cooper (1932), no other research into the epiphyllous nature of the flower of Bougainvillea has been undertaken. Perhaps this is due to the fact that most studies which have included Bougainvillea are comparative and speculated on the phylogenetic affinities of the Nyctaginaceae. Since Bougainvillea is the only genus of this family which exhibits epiphylly, the development of this structure has generated little interest among these workers. However, the controversy over other epiphyllous species, and epiphylly in general, has been lengthy.

The classical shoot theory specifies that flowers must arise from a stem (caulome) in the axil of its subtending bract (phyllome). Situations such as that found in Bougainvillea, where the mature flower is found on the adaxial surface of a colored bract would then be explainable only in terms of congenital fusion. Congenital, or phylogenetic fusion (also called concrescence, adnation, and connation), is a process which is nonobservable during ontogeny, but in which separate structures have gradually grown together or become 'fused' over the course of the evolution of the plant. This definition would then include such cases as those observed in a hooded genotype of barley (Stebbins and Yagil, 1966), in Chrysalidocarpus (Fisher, 1973), and in Phyllonoma integerrima (Dickinson and Sattler, 1974), where the rudimentary floret, branch, and inflorescence axis respectively, are all initiated epiphyllously.

However, in species such as Bougainvillea, where the flower has an axillary origin, workers wishing to interpret the mature epiphyllous condition in terms of the classical theory, would describe a developmental congenital fusion. Thus, Croizat-Chaley (1973), Stebbins (1950), Cusick (1966) and van Heel (1969), postulate the 'fusion' or incomplete separation of floral and leaf primordia, with intercalary growth eventually occurring beneath their common base. Perhaps this is the mechanism which Cooper (1932:815) had in mind when he wrote: "The individual flowers appear as club-shaped masses of cells in the axils of a partially developed bract. As the bract grows, each pedicel which remains attached adnate to the mid-vein of the adjacent bract elongates, so when the flower is mature it appears to have arisen from the upper surface of the bract." However, Cooper does not state how the flower and bract might have become 'adnate' nor does he speculate about the mechanism of elongation of the adnate flower pedicel and adjacent bract.

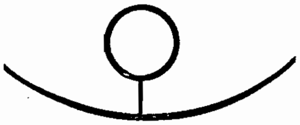
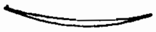
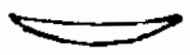
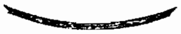
The concept of congenital fusion, whether applied to epiphylly or the gynoecium, has always been closely connected with studies of vascular anatomy. Traditional morphologists believe that changes in vascular anatomy "may reveal the former boundaries, relative positions, numbers, and categories of organs or their parts which may be obscured by reduction, connation, and adnation." (Moseley, 1967:160) Since there are separate vascular traces running to the flower and the floral bract of *Bougainvillea* from the inflorescence stele, vascular conservatists would point to this pattern as supportive of the theory of congenital fusion. However, not all epiphyllous flowers or inflorescences exhibit the vascular anatomy seen in *Bougainvillea*. In the majority of cases, the vascular anatomy seen within the leaf petiole or lamina midrib consists of two compartments - adaxial and abaxial. The adaxial component runs to the inflorescence, while the abaxial part continues to the remainder of the leaf. Such has been demonstrated in the epiphyllous inflorescences of *Erythrochiton hypophyllanthus* (Planchon, 1853), *Polycardia lateralis* (C. de Candolle, 1890), and *Tilia* (Arber, 1950), in the sterile and fertile leaves of *Phyllonoma integerrima* (Dickinson and Sattler, 1974) and in the fertile leaves only of *Helwingia japonica* (Dickinson and Sattler, 1975). As was noted above, the vasculature to the sterile and fertile leaves of *Phyllonoma* was found to be the same (Dickinson and Sattler, 1974). This is also true of members of the *Dichapetalaceae* with epiphyllous inflorescences (Prance, 1972). However, Dickinson and Sattler (1975) found different vascular anatomy in the sterile and fertile leaves of *Helwingia*. Such variety in vasculature between different genera has led Carlquist (1969), Schmid (1972), as well as others, to question the usefulness of the principle of vascular conservatism in determining homologies, degree of primitiveness, or ancestral condition.

Besides Cooper's (1932) study which included a brief developmental look at epiphyllous *Bougainvillea*, only Joshi and Rao (1934:182) have referred to the fact that "flowers in this genus are adnate for some distance with the bract"; while Gillis (1976:35) states: "The flowers are borne singly on the adaxial surface of the bract." Developmental studies of *Bougainvillea* lead me to concur with Cooper (1932) insofar as it is clear that each flower is indeed initiated in the axil of a young floral bract. Thereafter, an intercalated zone consisting of a basal intercalary meristem beneath the flower and bract primordia begins to produce derivative cells above. These cells eventually become vacuolated and are seen as long files throughout the flower and bract regions (Plate II, Figs. C,D). A similar mechanism of growth has been observed in epiphyllous inflorescences of *Hellwingia japonica* (Dickinson and Sattler, 1975).

Therefore, an intercalary meristem which gradually extends across the base of the two primordia from bract to flower, accounts for the epiphyllous position of the flower of *Bougainvillea*. This occurs independently of any 'fusion' between the separate floral and bract primordia. The above mechanism contrasts with the vegetative leaf development. Here one finds no evidence of a basal intercalary meristem extending across the leaf to the vicinity of the axillary bud.

It should be noted that these results of epiphylly do not exclude the interpretation of this flower within the bounds of 'congenital fusion'. However, it would seem unnecessary to invoke such a concept when a developmental mechanism producing the epiphyllous flowers of Bougainvillea is so clearly observable.

SYMBOLS USED IN INFLORESCENCE AND FLORAL DIAGRAMS

	inflorescence bract
	one epiphyllous flower of *Bougainvillea* on its floral bract
	floral bract
	tepal
	petal
	sepal
	single ovule in unistylar gynoecium
	stamen

ABBREVIATIONS USED IN PLATES AND LEGENDS

V	vegetative apex
R	inflorescence apex
RB	inflorescence bract
FB	floral apex
F	floral bract
L	vegetative leaf
Ab	axillary bud
P	tepal
K	sepal
C	petal
A	stamen
G	gynoecial wall
O	ovule
I_i	inner integument
I_o	outer integument

Number of Primordia Initiated:

Angle (in degrees) Between Primordia:	2P	3P	4P	5P	5P 4A	5P 5A	5P 6A	5P 7A	8A	# of buds studied	total average angle (degrees)
*P1-P2	142	124	147	149	144	145	142	141	-perianth removed---	38	144
P2-P3		138	135	130	148	141	142	144		35	141
P3-P4			153	153	141	148	147	149		34	147
P4-P5				136	142	136	137	138		27	138
P5-A1					152	135	143	147		26	144
*A1-A2					133	141	135	133	129	28	136
A2-A3					134	135	124	124	130	25	130
A3-A4					140	142	138	136	137	28	138
A4-A5						137	136	132	130	22	135
A5-A6							124	130	139	13	129
A6-A7								141	137	16	140
A7-A8									128	12	128

*P = tepal primordium
A = stamen primordium

TABLE I. ANGLES BETWEEN SUCCESSIVE FLORAL PRIMORDIA

LITERATURE CITED

ARBER, A., 1950. The Natural Philosophy of Plant Form. Cambridge.

BARNARD, C., 1957a. Floral histogenesis in the monocotyledons I. The Gramineae. Aust. J. Bot. 5:1-20.

______, 1957b. Floral histogenesis in the monocotyledons II. The Cyperaceae. Aust. J. Bot. 5:115-128.

______, 1958. Floral histogenesis in the monocotyledons III. The Juncaceae. Aust. J. Bot. 6:285-298.

BHARGAVA, H.R., 1932. Contributions to the morphology of _Boerhaavia_ _repanda_. J. Ind. Bot. Soc. 11:303-326.

______, 1952. The anatomy of the flower of _Boerhaavia_ _repanda_. Am. Midl. Nat. 47:508-512.

BUGNON, F., 1958. Eléments d'un chapitre complexe de morphologie végétale: les déformations nodale de la pousse par croissance intercalaire longitudinale chez les plantes â fleurs. Bull. Scient. Bourgogne 19:26-69.

CANDOLLE, A.P. de, 1813. Théorie élémentaire de la Botanique. Paris.

______, 1827. Organographie Végétale. 2 vols. Paris.

CANDOLLE, C. de, 1890. Recherches sur les inflorescences épiphylles. Mém. Soc. Phys. Hist. Nat. Genéve suppl. 6:1-37.

CARLQUIST, S., 1969. Towards acceptable evolutionary interpretations of floral anatomy. Phytomorphology 19: 332-362.

COOPER, D.C., 1932. The anatomy and development of the floral organs of _Bouginvillea_ _glabra_. Am. J. Bot. 19:814-822.

CROIZAT, L., 1960. Principia Botanica Volume Ia. Caracas: by the author.

CROIZAT-CHALEY, L., 1973. En torno al concepto de hoja ensayo de botanica analitica y sintetica. Biblioteca de la Academia de Ciencias Fisicas, Matematicas y Naturales, Caracas, 12.

CUSICK, F., 1966. On phylogenetic and ontogenetic fusions. In E.G. Cutter (Ed.), Trends in plant morphogenesis. London: Longmans.

Dickinson, T.A., 1978. Epiphylly in Angiosperms. Bot. Review 44:181-282.

DICKINSON, T.A., and SATTLER, R., 1974. Development of the epiphyllous inflorescence of _Phyllonoma integerrima_ (Turcz.) Loes.: Implications for comparative morphology. Bot. J. Linn. Soc. 69:1-13.

______, 1975. Development of the epiphyllous inflorescences of _Helwingia japonica_ (Helwingiaceae). Am. J. Bot. 62(9):962-973.

DOUGLAS, G.E., 1944. The inferior ovary. Bot. Review 10(3): 125-186.

DUCHARTRE, P., 1886. Note sur un Bégonia nouveau, à inflorescences épiphylles (_Begonia ameliae_ Bruant). J. Soc. natn. Hort Fr. 8:153-169.

EAMES, A.J., 1961. Morphology of the Angiosperms. New York.

ECKARDT, Th., 1954. Morphologische und systematische Auswertung der Placentation von Phytolaccaceen. Ber. deutsch. bot. Ges. 67:113-128.

J.B., 1973. Unusual branch development in the palm _Chrysalidocarpus_. Bot. J. Linn. Soc. 66:83-95.

GILLIS, W.T., 1976. Bougainvilleas of cultivation (Nyctaginaceae). Baileya 20(1):34-41.

GREGOIRE, V., 1931. La valeur morphologique des carpelles dans les Angiospermes. Bull. Acad. Roy. Belgique. Cl. Sc. 17:1286-1302.

HACKETT, W.P. and SACHS, R.M., 1968. Experimental separation of inflorescence development from initiation in _Bougainvillea_. Amer. Soc. Hort. Sci. 92:615-621.

HEEL, W.A. van, 1969. The synangial nature of pollen sacs on the strength of 'congenital fusion' and conservatism of the vascular bundle system with special reference to some Malvales. Proc. K. ned. Akad. Wet. (Ser. C) 72(2):172-205.

HEIMERL, A., 1889. In Engler and Prantl (Eds.), Die natürlichen Pflanzen-familien. 3, Abt. Ib:14-32.

ITERSON, G. van, 1907. Mathematische und mikroskopisch-anatomiche Studien über Blattstellungen. Jena.

JONG, K., 1970. Developmental aspects of vegetative morphology in Streptocarpus. Ph.D. Thesis, Univ. Edinburgh, Edinburgh, Scotland.

JOSHI, A.C. and RAO, V.S.R., 1934. Vascular anatomy of the flowers of four Nyctaginaceae. J. Indian Bot. Soc. 13:169-186.

KAM, Y.K., 1974. Developmental studies of the floret in Oryzopsis virescens and O. hymenoides (Gramineae). Can J. Bot. 52:125-149.

KLAUS, H., 1966. Ontogenetische und histogenetische Untersuchungen an der Gerste (Hordeum distichon L.) Bot. Jahrb. 85:45-79.

LAM, H.J., 1950. Stachospory and phyllospory as factors in the natural system of the Cormophyta. Sven. bot. Tidskr. 44:517-534.

LAM, H.J., 1959. Taxonomy, General Principles and Angiosperms. In W.B. Turrill (Ed .), Vistas in Botany. 1:3-75. London.

LORCH, J., 1963. The Carpel - A Case History of an Idea and a Term. Centaurus 8:269-291.

MACDONALD, A.D., 1974. Theoretical problems of interpreting floral organogenesis of Laportea canadensis. Can. J. Bot. 52:639-644.

MACDONALD, A.D. and SATTLER, R., 1973. Floral development in Myrica gale and the controversy over floral concepts. Can. J. Bot. 51:1965-1975.

MAHESHWARI, P., 1929. Contributions to the morphology of Boerhaavia diffusa. (I). J. Indian bot. Soc. 8:219-234.

MAHESHWARI, P., 1930. Contributions to the morphology of Boerhaavia diffusa. (II) J. Indian bot. Soc. 9:42-60.

MAZE, J., DENGLER, N.G. and BOHM, L.R., 1971. Comparative floret development in Stipa tortilis and Oryzopsis milaceae (Gramineae). Bot. Gazette 132:273-298.

MAZE, J., BOHM, L.R. and BEIL, C.E., 1972. Studies on the relationships and evolution of supraspecific taxa utilizing developmental data. I. Stipa lemmonii (Gramineae). Can. J. Bot. 50:2327-2352.

MCLEAN, R.C. and IVIMEY-COOKE, W.R., 1951. Textbook of Theoretical Botany I. London: Longmans.

MEHLENBACHER, L.E.,Jr., 1970. Floret development, embryology, and systematic position of Oryzopsis hendersoni (Gramineae). Can. J. Bot. 48:1741-1758.

MELVILLE, R., 1962. A new theory of the Angiosperm flower I. The gynoecium. Kew Bull. 16:1-50.

MEEUSE, A.D.J., 1966. Fundamentals of Phytomorphology. The Ronald Press Co., New York.

______, 1973. Some Fundamental Principles in Interpretive Floral Morphology. In Varghese, T.M. (Ed.), Vistas in Plant Sciences. Volume I. Hissar, India.

MOELIONO, B.M., 1970. Cauline or Carpellary Placentation among Dicotyledons I. The Cauline Ovules of Centrosperms, text. Koninklijke Van Gorcum and Co. N.V., Assen. The Netherlands.

MOSELEY, M.F., Jr., 1967. The value of the vascular system in the study of the flower. Phytomorphology 17: 159-164.

PANKOW, H., 1962. Histogenetische Studien an den Blüten einiger Phanerogamen. Bot. Stud. 13:1-106.

PARKIN, J., 1955. A plea for a simpler gynoecium. Phytomorphology 5:46-57.

PAYER, J.B., 1857. Traité d'organogénie comparée de la fleur. Paris.

PLANCHON, J.E., 1853. Quelques notes sur les inflorescences épiphylles à l'occasion d'une éspèce nouvelle d'Erythrochiton. Mems. Acad. Stanislas, Nancy.

PRANCE, G.T., 1972. Dichapetalaceae. Flora Neotropica, Monograph #10.

PURI, V., 1952. Placentation in Angiosperms. Bot. Review 18:603-651.

RODIN, R.J. and DAVIS, R.E., 1967. The use of papain in clearing plant tissues for whole mounts. Stain Tech. 42(4):203-206.

ROHWEDER, O., 1967. Karpellbau und Synkarpie bei Ranunculaceen. Ber. schweiz. bot. Ges. 77:376-430.

ROHWEDER, O. and HUBER, K., 1974. Centrospermen-Studien VII. Beobachtungen und Anmerkungen zur Morphologie und Entwicklungsgeschichte einiger Nyctaginaceen. Bot. Jahrb. Syst. 94(3):327-359.

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

______, 1973. Gynoecia without carpels. Am. J. Bot. 60: suppl. pg. 36.

______, 1974a. A new approach to gynoecial morphology. Phytomorphology 24:22-34.

______, 1974b. A new conception of the shoot of higher plants. J. theor. Biol. 47:367-382.

SCHMID, R., 1972. Floral bundle fusion and vascular conservatism. Taxon 21(4):429-446.

SHARMA, H.P., 1963a. Contributions to the morphology of the Nyctaginaceae I. Anatomy of the node and inflorescence of some species. Proc. Ind. Acad. Sci. 57:35-50.

SHARMA, H.P., 1963b. Contributions to the morphology of the Nyctaginaceae II. Floral anatomy of some species. Proc. Ind. Acad. Sci. 57:149-163.

SHARMAN, B.C., 1960. Developmental anatomy of the stamen and carpel primordia in Anthoxanthum odoratum. L. Bot. Gazette. 121:192-198.

SNOW, M. and SNOW, R., 1948. A new theory of leaf formation. Nature 162:798.

STEBBINS, G.L., 1950. Variation and evolution in plants. New York: Columbia University Press.

STEBBINS, G.L. and YAGIL, E., 1966. The morphogenetic effects of the hooded gene in barley. I. The course of development in hooded and awned genotypes. Genetics 54(3):727-741.

TIEGHEM, Ph. van, 1875. Recherches sur la structure du pistil et sur l'anatomie comparée de la fleur. Mém. Ac. Inst. Imp. de France 21:1-261.

TROLL, W., 1939. Die morphologische Natur der Karpelle. Chron. Bot. 5:38-41.

WARDLAW, C.W., 1968. Morphogenesis in Plants. Methuen and Co. Ltd. London.

WIBAUT, C., 1965. Ontogenèse des organes végétatifs et réproducteurs du Mirabilis jalapa L. (Nyctaginacées). Rev. Cytol. et Biol. Vég. 28:43-161.

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

ZIMMERMANN, W., 1965. Die Telomtheorie. Stuttgart.

FIGURE I

Diagrammatic representation of the inflorescence of *Bougainvillea spectabilis* Willd.

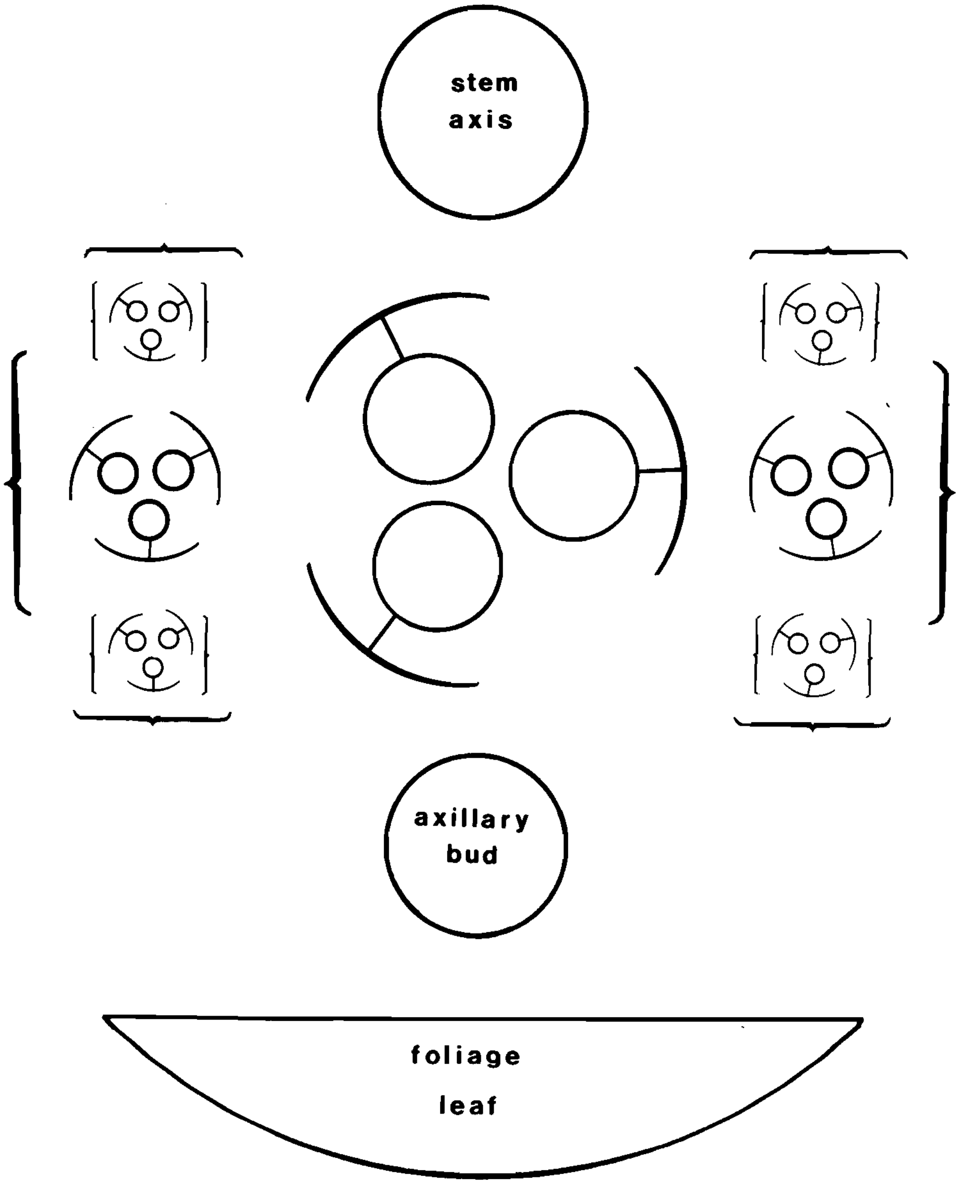
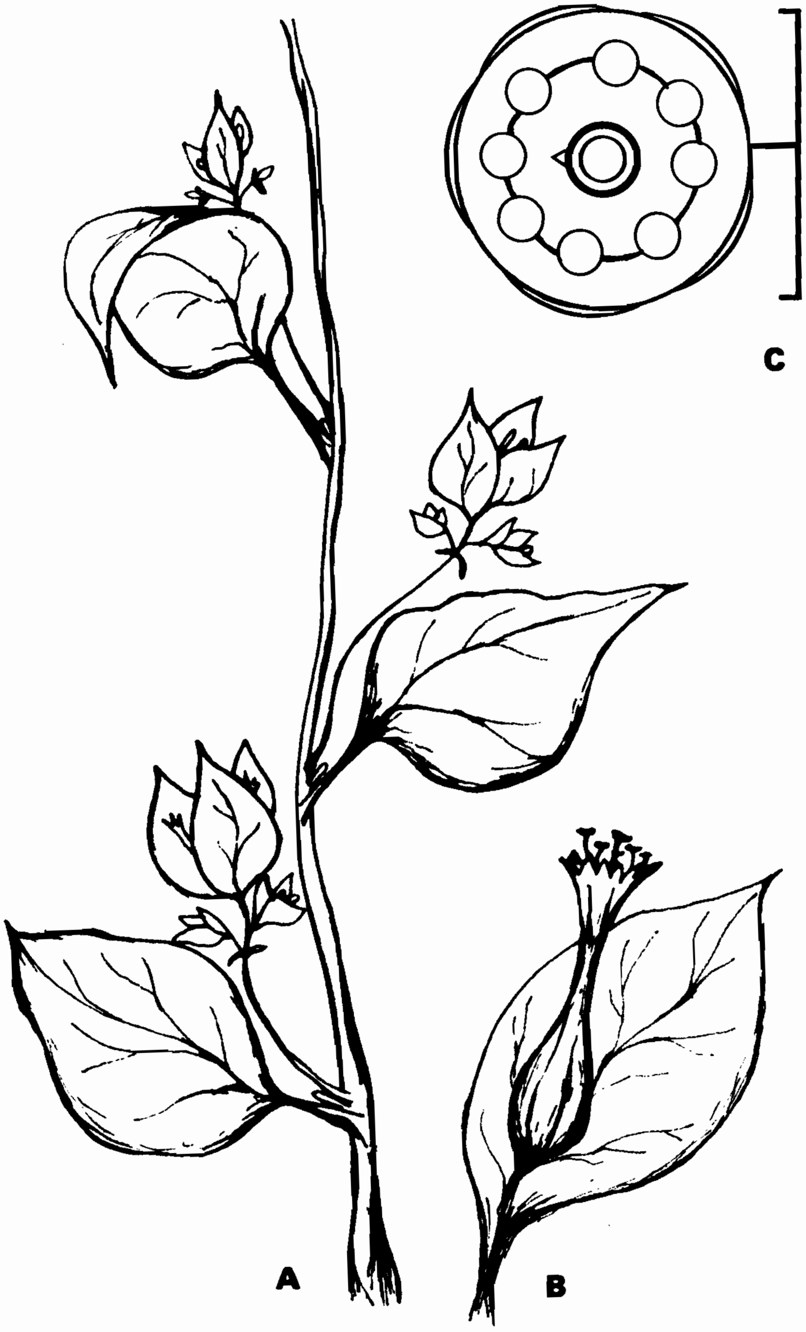

stem axis
axillary bud
foliage leaf

FIGURE II

A. Sketch of the growth habit of <u>Bougainvillea</u> during inflorescence production.

B. Detail of one mature flower situated epiphyllously on the adaxial surface of a colored bract.

C. Floral diagram.



Bougainvillea spectabilis Willd.

PLATE I. FIGURES A-E

Fig. A Oblique view of an inflorescence apex (R) subtended by the first inflorescence bract (RB_1). The second inflorescence bract (RB_2) is initiating. X228

Fig. B.E Inflorescence bracts removed.

Fig. B Top view of an inflorescence apex around which the first two floral bract primordia (FB_1 and FB_2) are developing, while the third floral bract (FB_3) is being initiated. X228

Fig. C Side view of an inflorescence showing the initiation of the first (F_1) and third (F_3) floral buds in the axils of their respective floral bracts. Also seen is the second floral bract (FB_2) obscuring the second floral bud. X228

Fig. D Side view of an inflorescence at a slightly older stage than that of Fig. C showing the second (F_2) and third (F_3) floral buds developing in the axils of their respective floral bracts. Also seen is the first floral bract obscuring the first floral bud. X228

Fig. E Oblique view of a young inflorescence composed of its three floral buds. The first and second floral bracts have been removed. X228

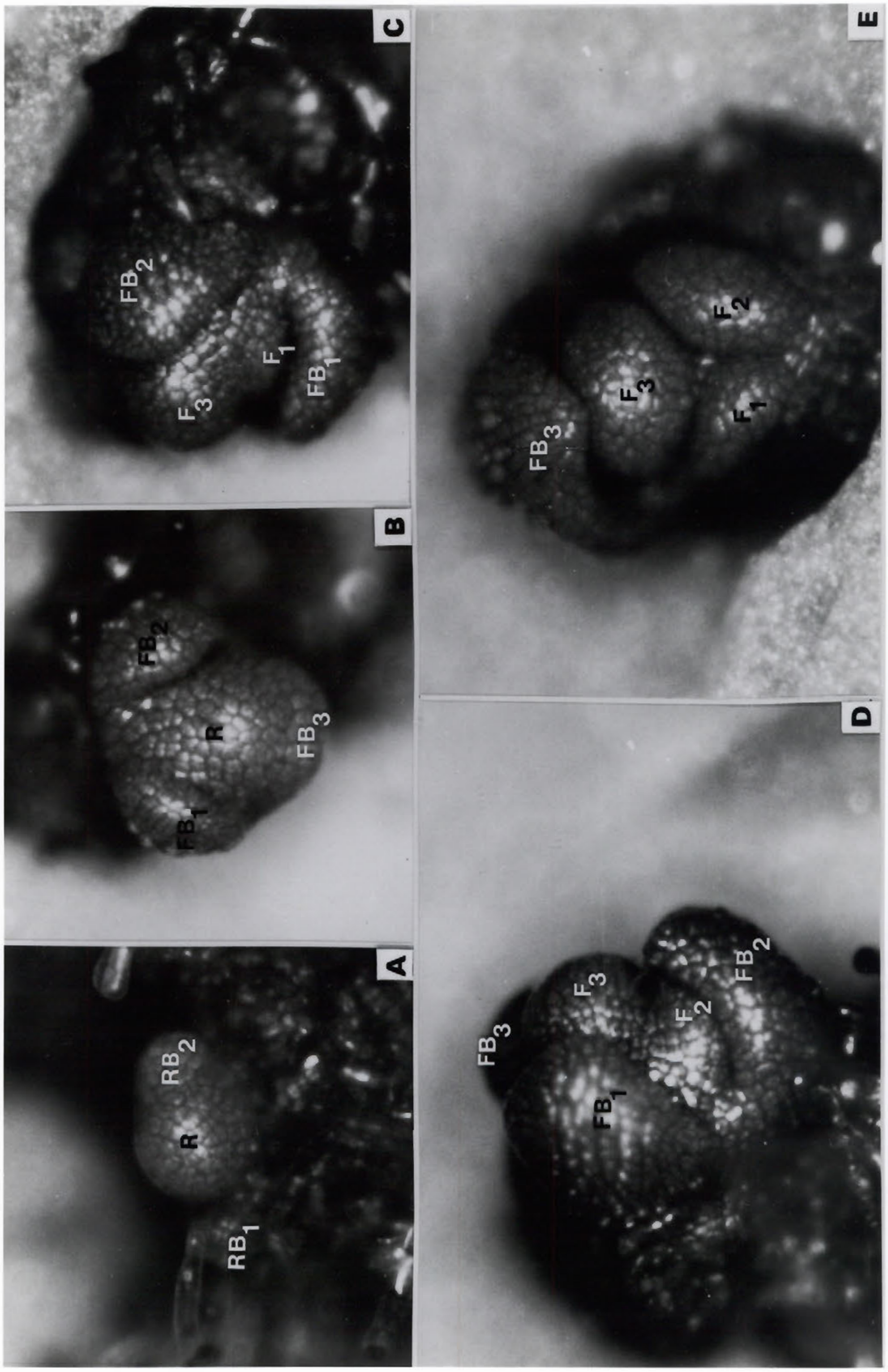

A
R
RB_1
RB_2
B
R
FB_1
FB_2
FB_3
C
FB_1
FB_2
F_1
F_3
D
FB_1
FB_2
FB_3
F_2
F_3
E
FB_3
F_1
F_2
F_3

PLATE II. FIGURES A-E

Figs. A-D Median longitudinal sections through successively older floral apices and their subtending bracts.

Fig. A A young floral apex (F) developing in the axil of its floral bract (FB). At this stage the floral bract is completely meristematic throughout. Developing procambial strands to the bract can be seen. X224

Fig. B A slightly older floral apex, still in the axil of its subtending bract. Perianth primordia are initiating, and the cells in the abaxial portion of the bract already appear larger and more vacuolated than those in the adaxial region of the bract. Note that procambial strands are now developing towards the floral apex. X224

Fig. C A floral apex at the stage where stamen primordia are initiating, showing a young intercalated zone below the point of insertion of the floral bud and bract. X224

Fig. D A well developed intercalated region below the junction of flower bud and bract as evidenced by the longitudinal files of cells throughout the entire bract and floral regions. X140

Fig. E Clearing of a mature flower and floral bract showing separate vascular traces from the inflorescence peduncle to the flower (arrow) and the floral bract (double arrow) respectively. X8

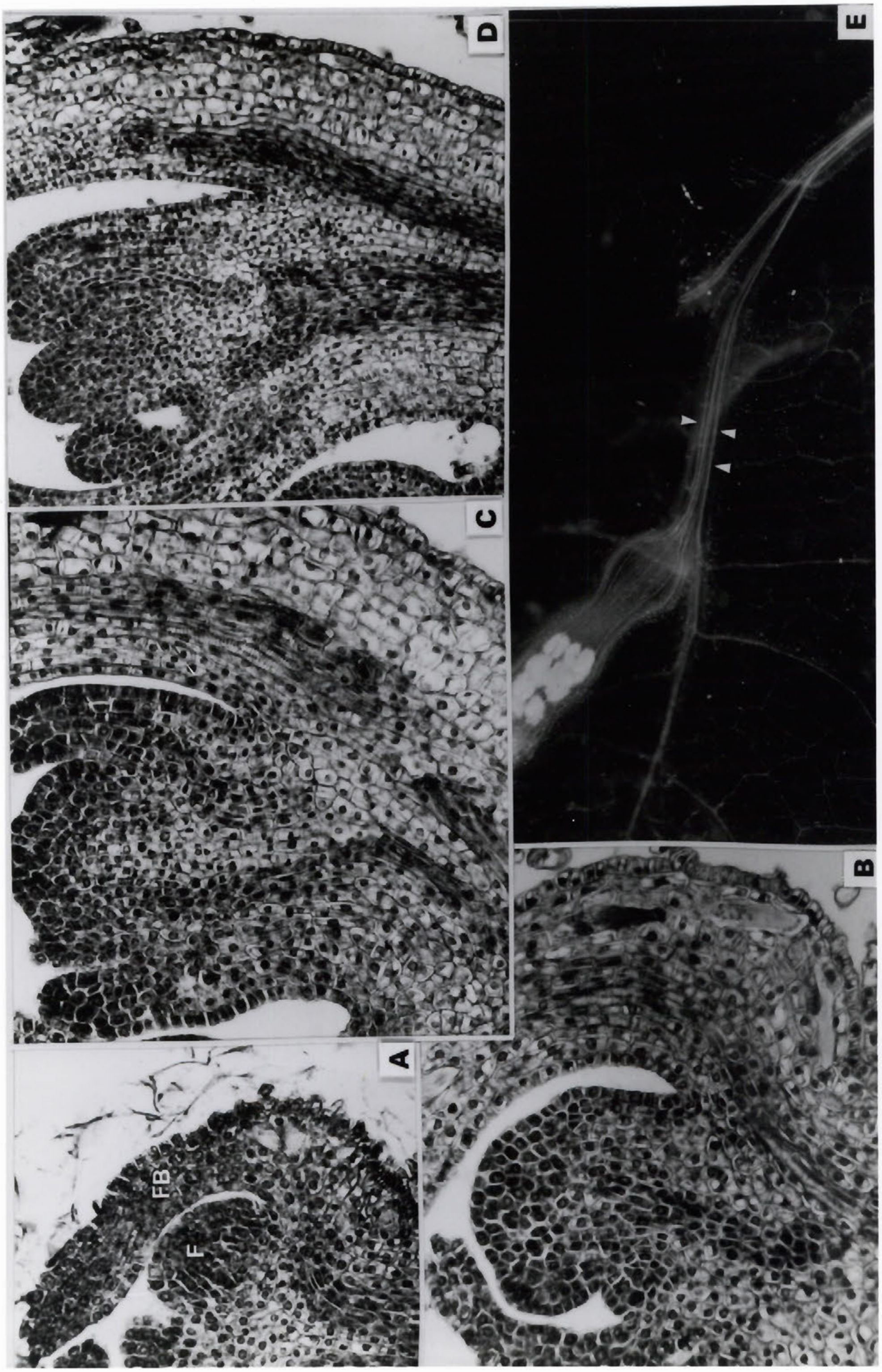

A
FB
F
B
C
D
E

PLATE III. FIGURES A-F

Figs. A-F Top views of floral buds showing sequential initiation of perianth (P) and stamen (A) primordia. The floral bracts have been removed. Perianth and stamen primordia are numbered in their order of appearance. X228

Fig. C Growth occurs between the first four perianth primordia to produce a young perianth tube. X228

Fig. D The fifth stamen primordium (P_5) is initiated directly on the perianth tube.

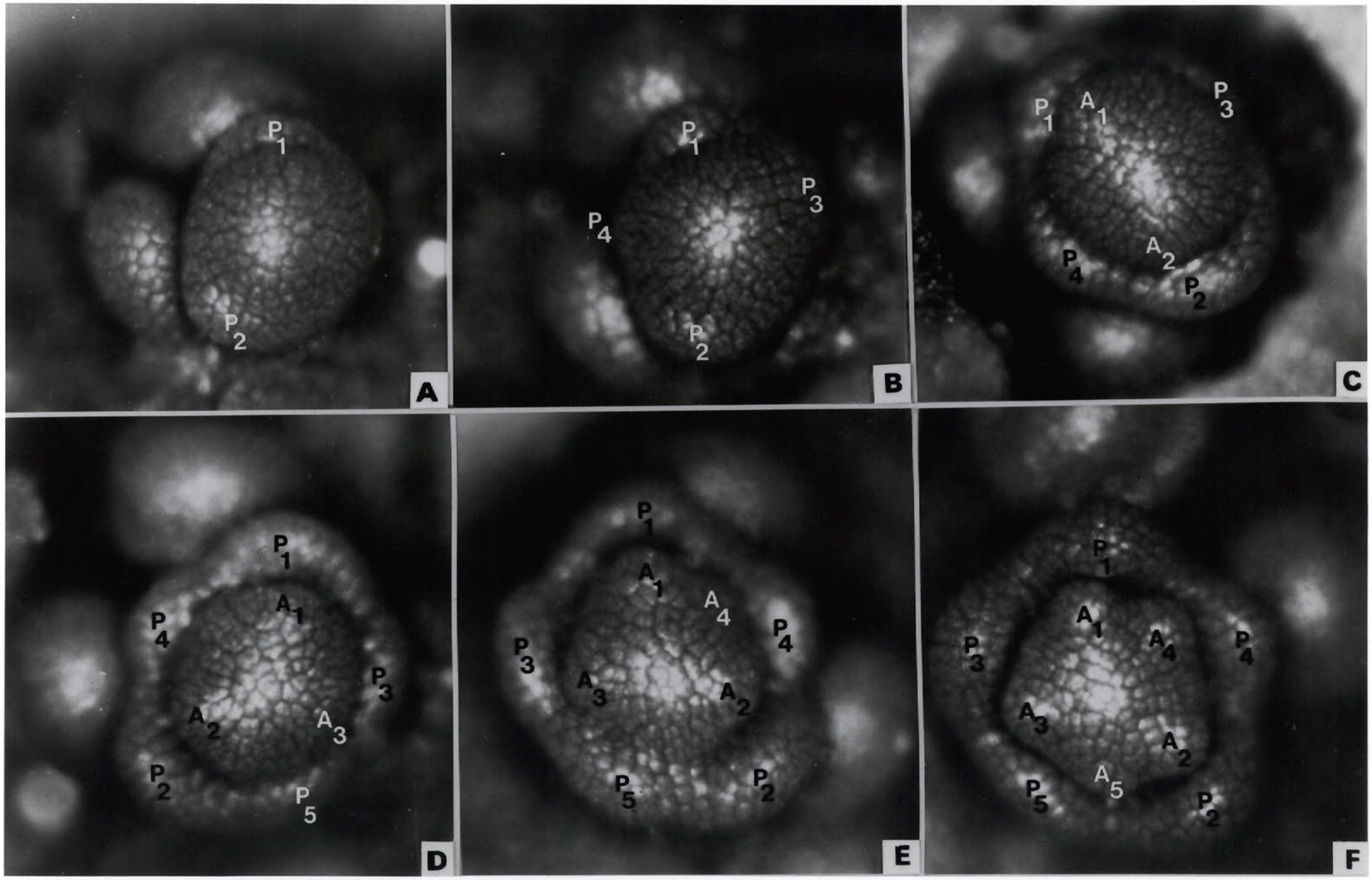

P1
P2
A
P1
P3
P4
P2
B
P1
A1
P3
A2
P4
P2
C
P1
A1
P4
P3
A2
A3
P2
P5
D
P1
A1
A4
P4
P3
A3
A2
P5
P2
E
P1
A1
A4
P4
P3
A3
A2
A5
P5
P2
F

PLATE IV. FIGURES A-D

Figs. A-D	Top views of floral buds showing the continuation of sequential stamen initiation until the full complement of eight androecial members is present (Figs. C and D). X228
Figs. B,C	Gradual enlargement of the floral apex (F). X228
Fig. D	Growth occurs in a semicircular zone around the floral apex to produce the gynoecial wall (arrows). The tepals have been removed. X228

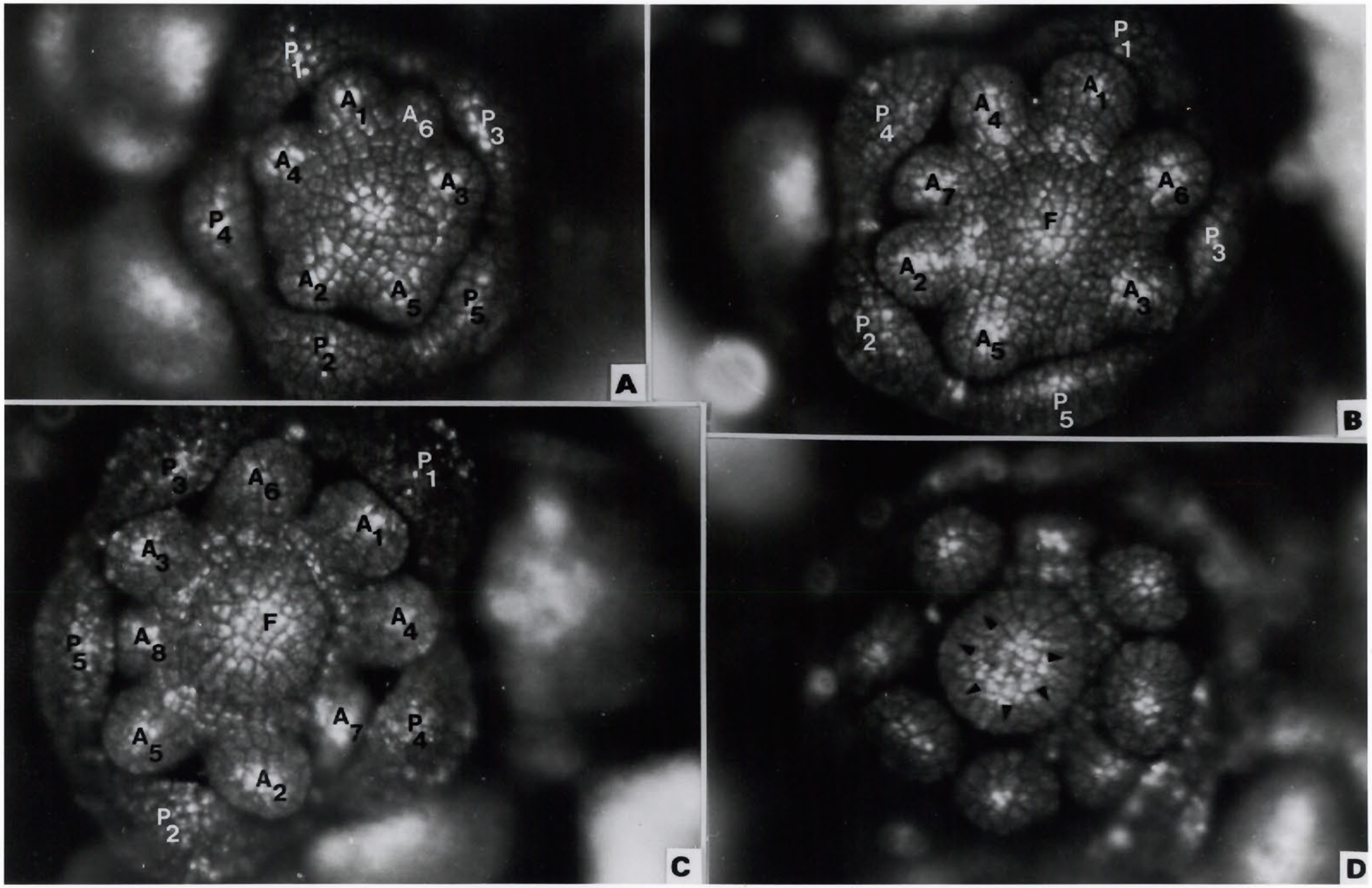

A
P1
A1
A6
P3
A4
A3
P4
A2
A5
P5
P2
B
P1
P4
A4
A1
A7
F
A6
P3
A2
A3
P2
A5
P5
C
P3
A6
P1
A1
A3
F
A4
P5
A8
A7
P4
A5
A2
P2
D

PLATE V. FIGURES A-D

Figs. A-D	Median longitudinal sections of young floral buds at different developmental stages. X400
Fig. A	A young floral apex (F) in the axil of its subtending floral bract (FB). X400
Fig. B	Initiation of perianth primordia (P). X400
Fig. C	Initiation of stamen primordia (A), and the gradual enlargement of the floral apex (F). X400
Fig. D	When the stamen primordia are all present, the floral apex enlarges and becomes somewhat dome-shaped. X400

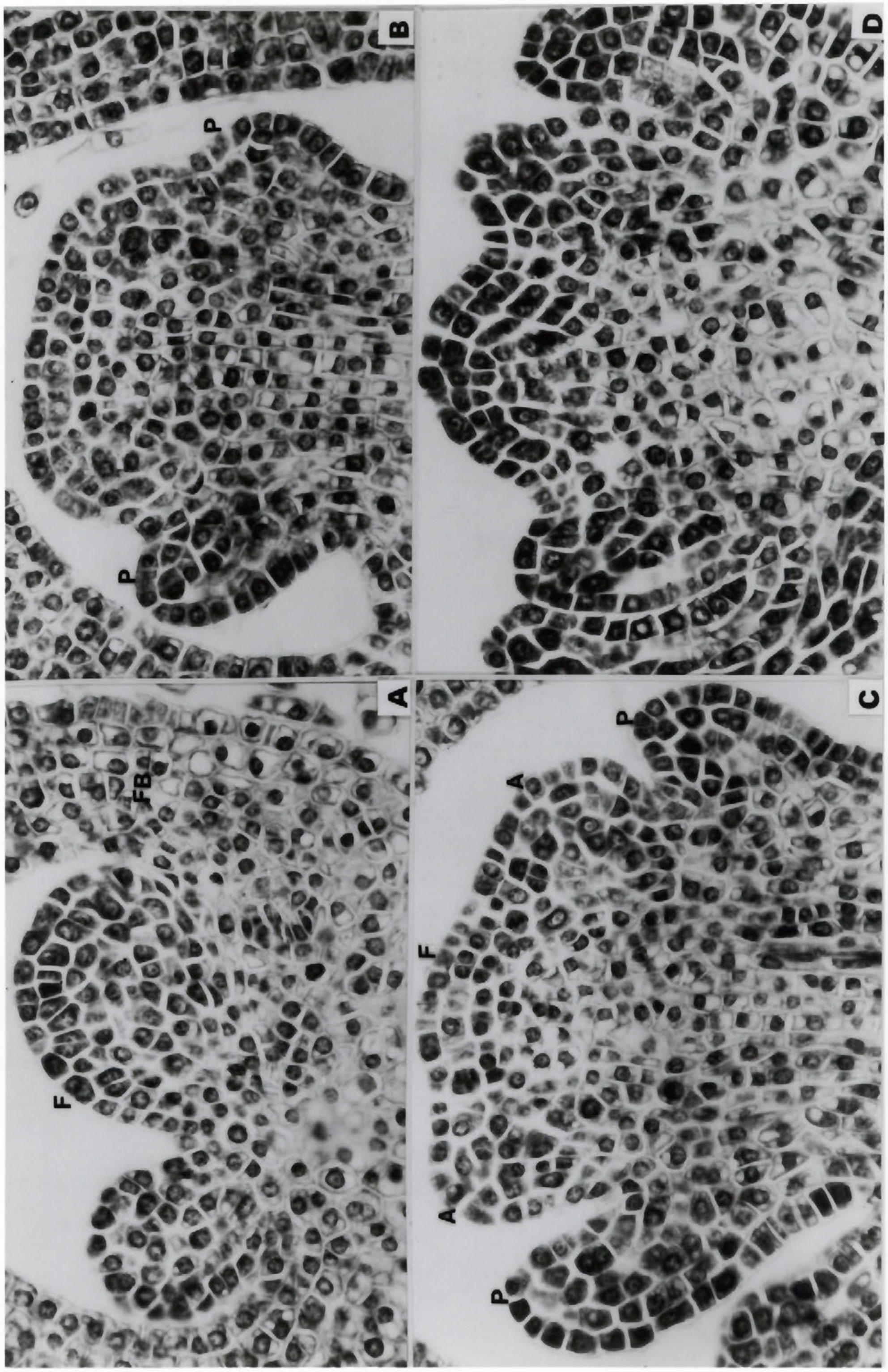

B
P
P
D
A
FB
F
C
P
A
F
A
P

PLATE VI. FIGURES A-H

Figs. A,C E,G	Side views of gynoecia at successively older stages of development. X228
Figs. B,D F,H	Median longitudinal sections of stages comparable to those in Figs. A,C,E and G, respectively. Figs. B,D X480; Figs. F,H X400. The tepals and stamens of the buds in Figs. A-H have been dissected away to reveal stages of gynoecial development.
Figs. A-D	Growth occurs in a semicircular zone to produce the gynoecial wall (G). Figs. A,C X228; Figs. B,D X480.
Figs. E,F	After elongation of the gynoecial wall, the floral apex is transformed into a basal and terminal ovule (O) in the centre of the gynoecial cavity. Fig. E X228; Fig. F X400.
Figs. G,H	Further upgrowth of the gynoecial wall and enlargement of the ovule ensues. Fig. G X228; Fig. H X400.

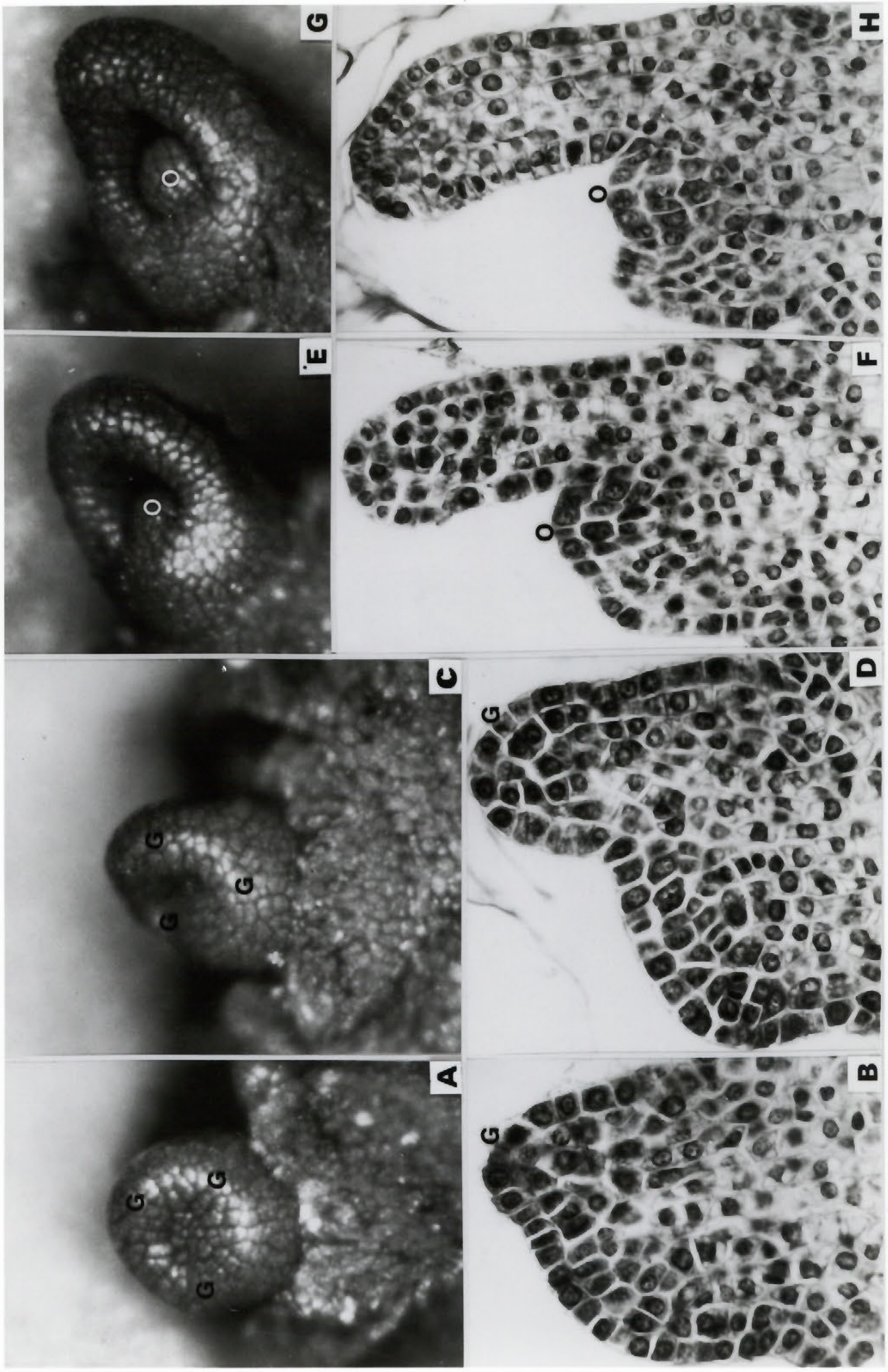

A
G
G
G
B
G
C
G
G
G
D
G
E
O
F
O
G
O
H
O

PLATE VII. FIGURES A-F

Fig. A	Side view of the gynoecium showing upgrowth of the dorsal portion of the gynoecial wall which will eventually become a short style. Closure of the gynoecial cavity occurs by the surface fusion of its lengthwise margins (arrows). X228
Fig. B	The gynoecial wall has been removed to show a slightly oblique view of the nucellus (N) surrounded by the inner (I_i) integument. The outer integument (I_o) is just being initiated. X228
Figs. C,D	Side views of successively older stages of ovule development than that seen in Fig. B. The two integuments are now well formed and enclose the nucellus. The ovule is beginning to curve so that the micropyle eventually faces away from the former gynoecial opening. X228
Figs. E,F	Clearings of a young (Fig. E) and a fully mature (Fig. F) gynoecium showing the long dorsal bundle (2 arrows) which supplies the gynoecial wall, and the short vascular trace entering the ovule ventrally (1 arrow). Note the basipetal lignification of these vascular strands. Fig. E X32; Fig. F X18.

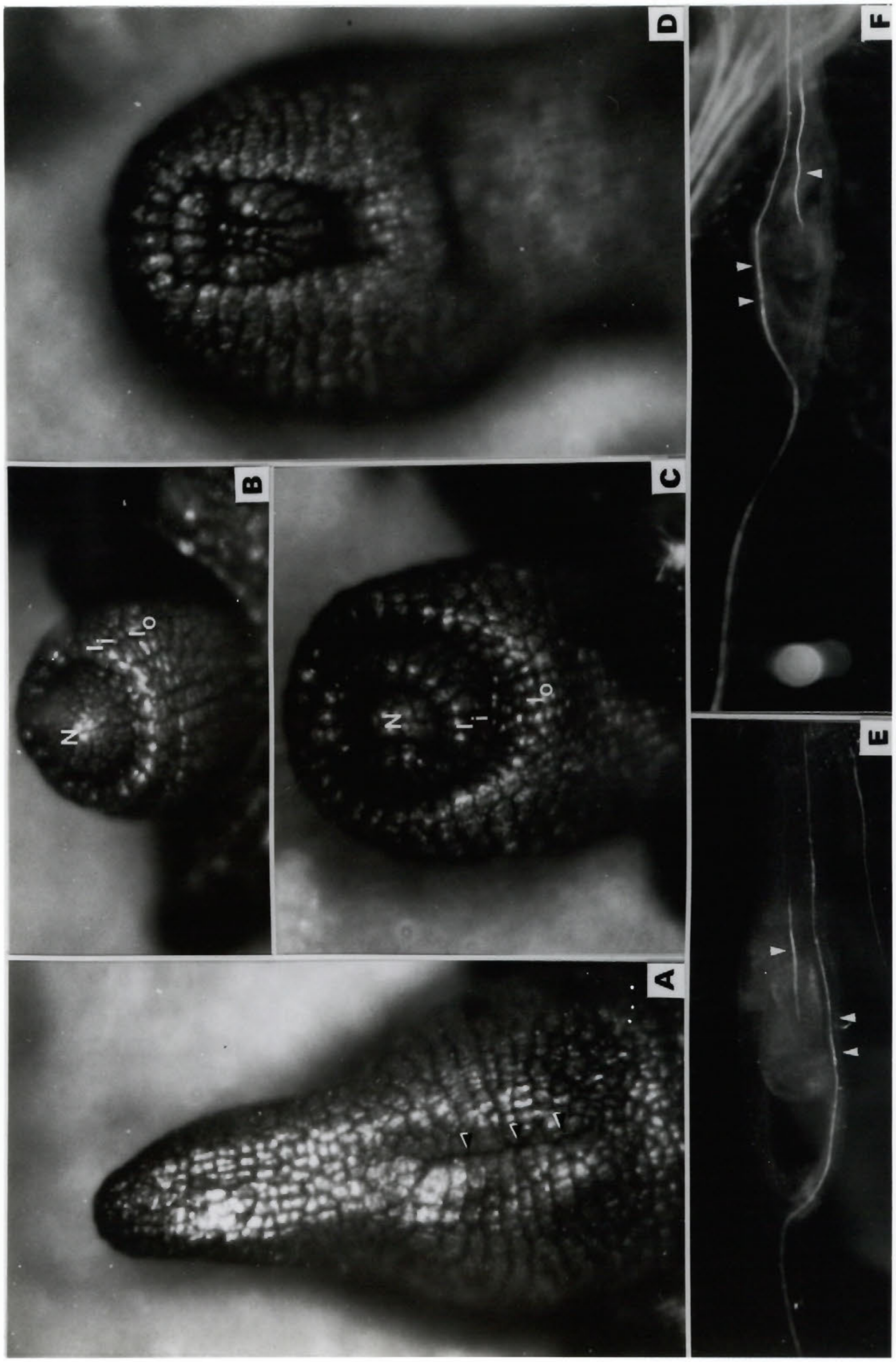

A
B
N
i
o
C
N
i
o
D
E
F

PLATE VIII. FIGURES A-E

Figs. A-D Median longitudinal sections through different shoot tips.

Fig. A A vegetative apex (V) showing the initiation of the youngest leaf primordium (L_1), and towards the other edge of the apex, an older developing leaf (L_2). At this stage L_2 is completely meristematic throughout, and the developing procambial strand to the leaf can be seen. Also present are two young axillary buds (Ab) in the axils of leaves L_3 and L_4. X224

Fig. B An older shoot apex and one vegetative leaf in which the cells of the abaxial region already appear larger and more vacuolated than those in the shoot tip and adaxial portion of the leaf. An axillary bud is initiating in the axil of this leaf. X224

Figs. C,D Two magnifications of an older vegetative leaf and its developing axillary bud than that seen in Fig. B. Growth of this leaf is occurring by prominent cell enlargement and vacuolation in the abaxial portion of the lamina. Fig. C X224; Fig. D X140.

Fig. E Clearing of a mature leaf showing several of the vascular bundles from the petiole which enter the leaf lamina and branch repeatedly to supply its length. X8

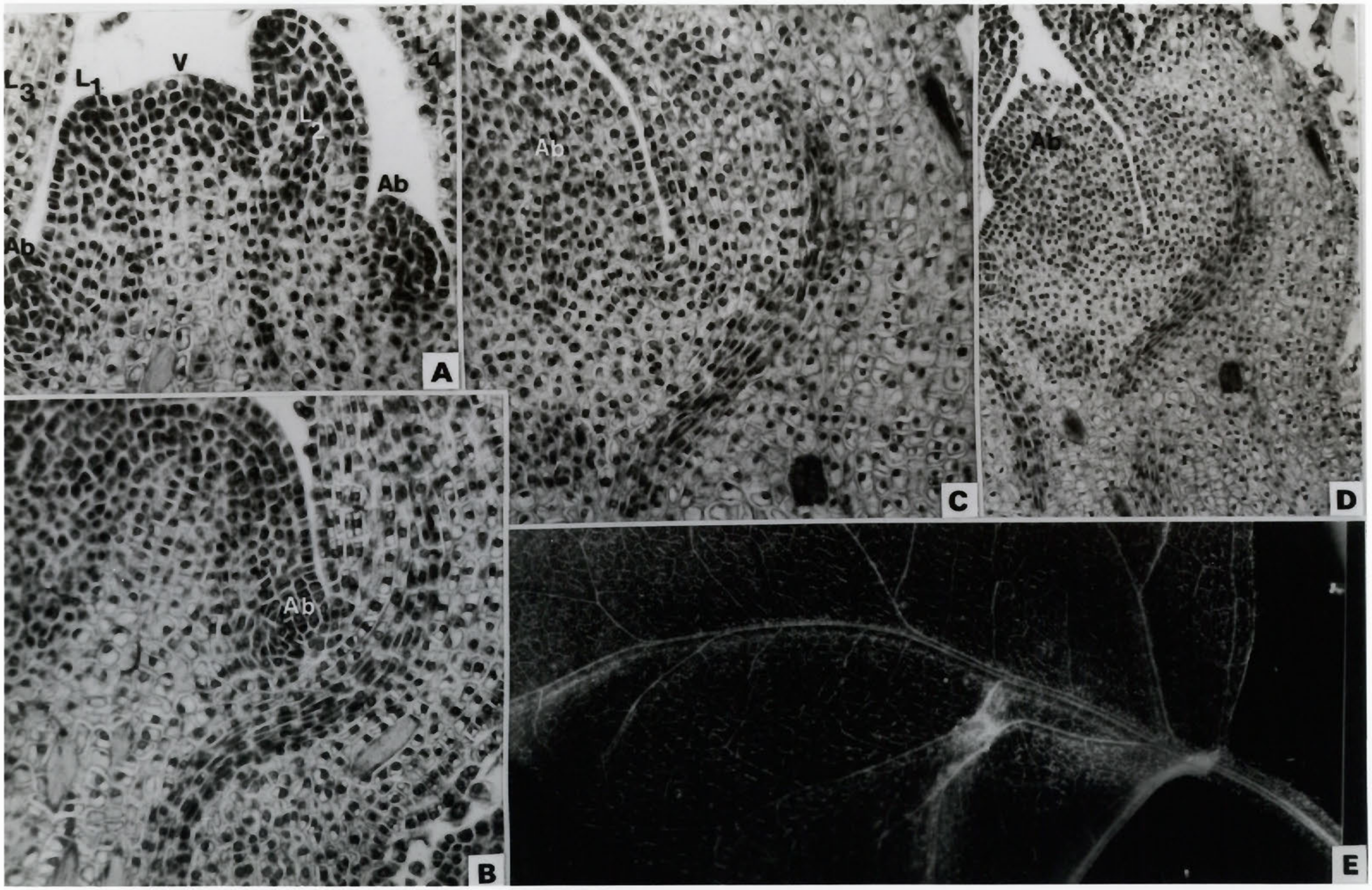
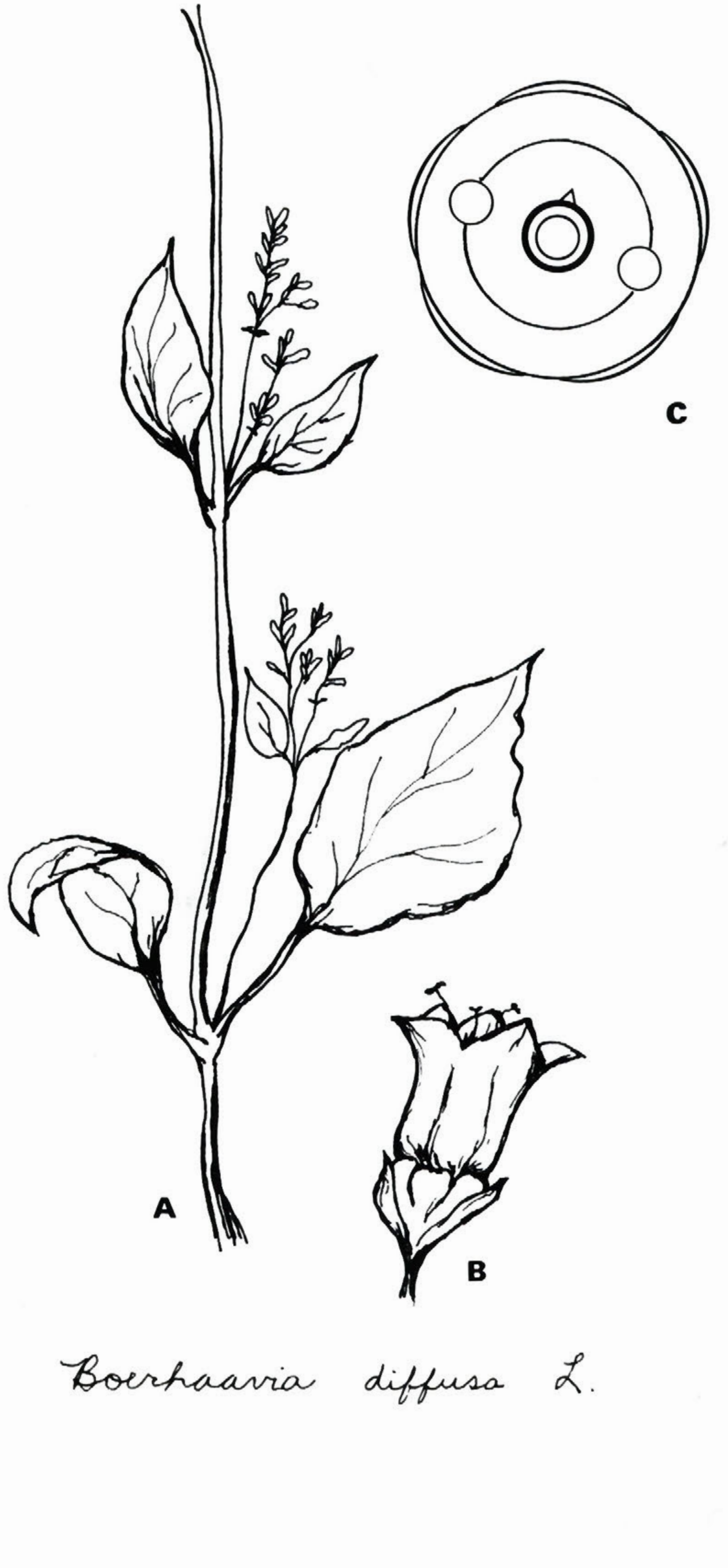

L3
L1
V
L2
L4
Ab
Ab
A
Ab
C
Ab
D
Ab
B
E

FIGURE III

A. Sketch of the growth habit of Boerhaavia during inflorescence production.

B. Detail of one mature flower.

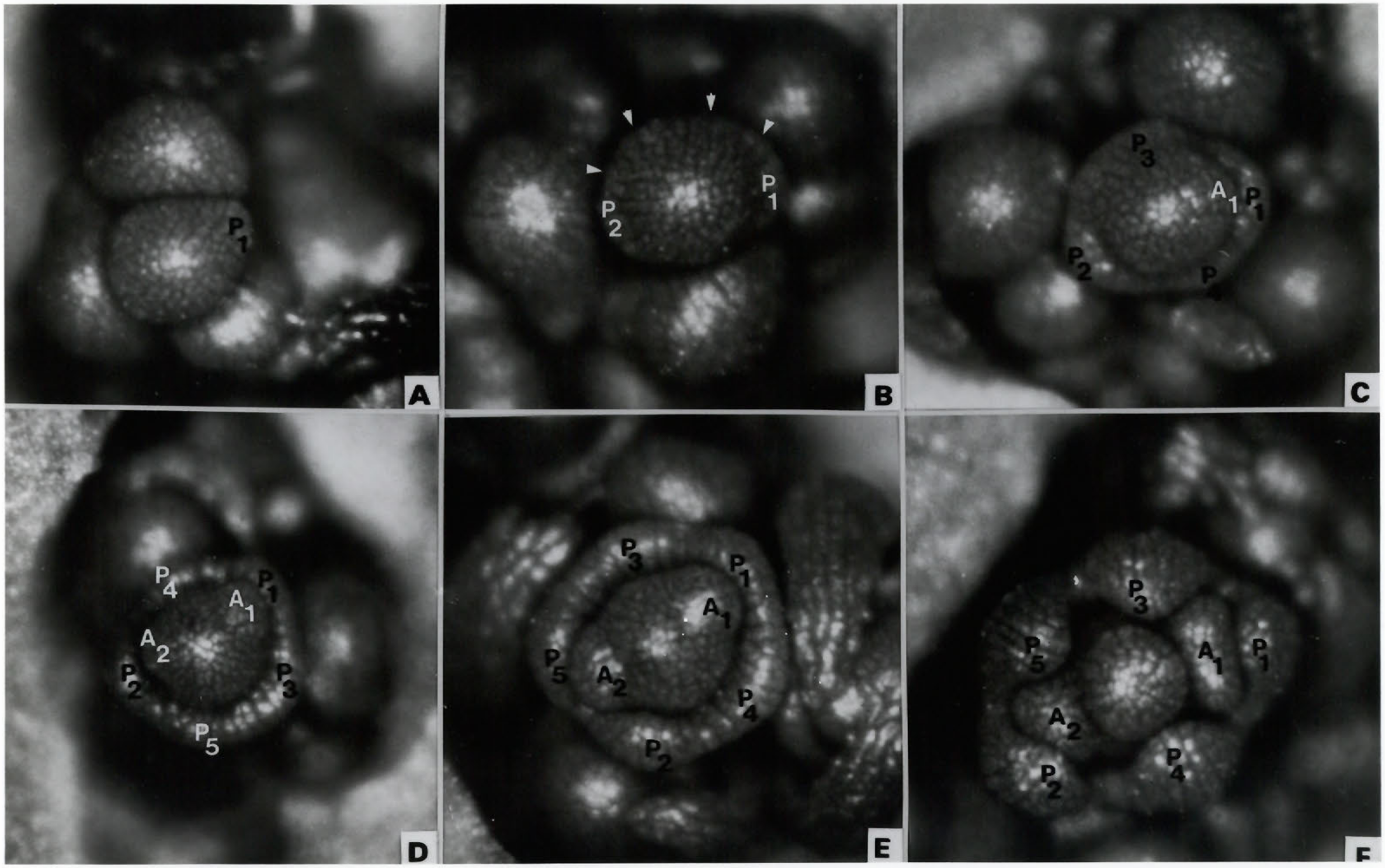
C. Floral diagram.



Boerhaavia diffusa L.

PLATE IX. FIGURES A-F

Figs. A-F	Top views of floral buds at successively older stages of development. X266
Fig. A	Initiation of the first perianth primordium (P_1). X266
Fig. B	A slightly older floral bud showing the initiation of the second perianth primordium (P_2), and growth occurring between these two tepal primordia (arrows) to produce the beginning of a perianth tube. X266
Fig. C	Further growth of the perianth tube, and the initiation of the third (P_3) and fourth (P_4) tepal primordia directly on the tube. Also seen is the initiation of the first stamen primordium (A_1) opposite tepal lobe one. X266
Fig. D	An older floral bud showing the initiation of the fifth tepal (P_5) on the perianth tube. Also seen is the development of the first stamen and the initiation of the second stamen primordium (A_2) alternate to tepals two and four. X266
Fig. E	The perianth and stamens are more developed. Note that in this floral bud the second stamen is in a position alternate to tepals two and five (compare with Fig. D). X266
Fig. F	A more mature floral bud in which the perianth tube and stamens are well developed. The floral apex has enlarged and become somewhat dome-shaped. X266



P1
A
P2
P1
B
P3
A1
P1
P2
P4
C
P4
A1
P1
A2
P2
P3
P5
D
P3
P1
A1
P5
A2
P4
P2
E
P3
P5
A1
P1
A2
P2
P4
F

PLATE X. FIGURES A-F

Fig. A An oblique view of a floral bud with the perianth removed showing the characteristic position of the two stamens and the developing gynoecium. Growth occurs in a semicircular zone around the periphery of the floral apex to produce the gynoecial wall (arrows). A single basal ovule (O) is initiated in a terminal position in the centre of the gynoecial cavity. X266

Fig. B An oblique view of a slightly older floral bud than that seen in Fig. A showing the elongation of the gynoecial wall and the terminal ovule. X266

Fig. C The stamens have been removed to show the elongation of the dorsal wall of the gynoecium into what will eventually be a long filiform style. The gynoecial cavity is closed by the surface fusion of its lengthwise margins (arrows). X266

Figs. D-F Top views of floral buds showing the variations in number of stamens initiated (Figs. D,E), and a case of differing stamen position (Fig. F) from that usually seen. X266

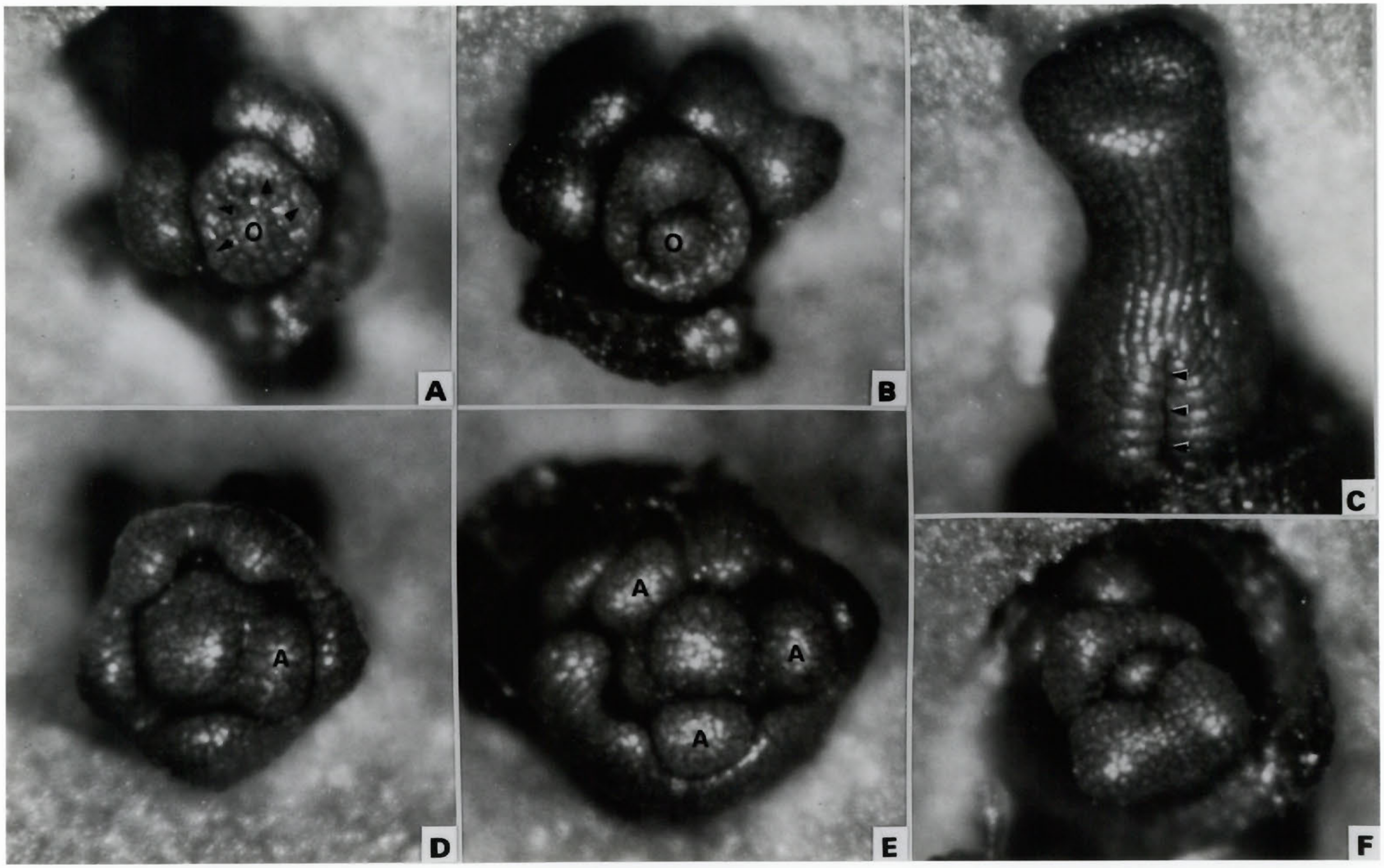
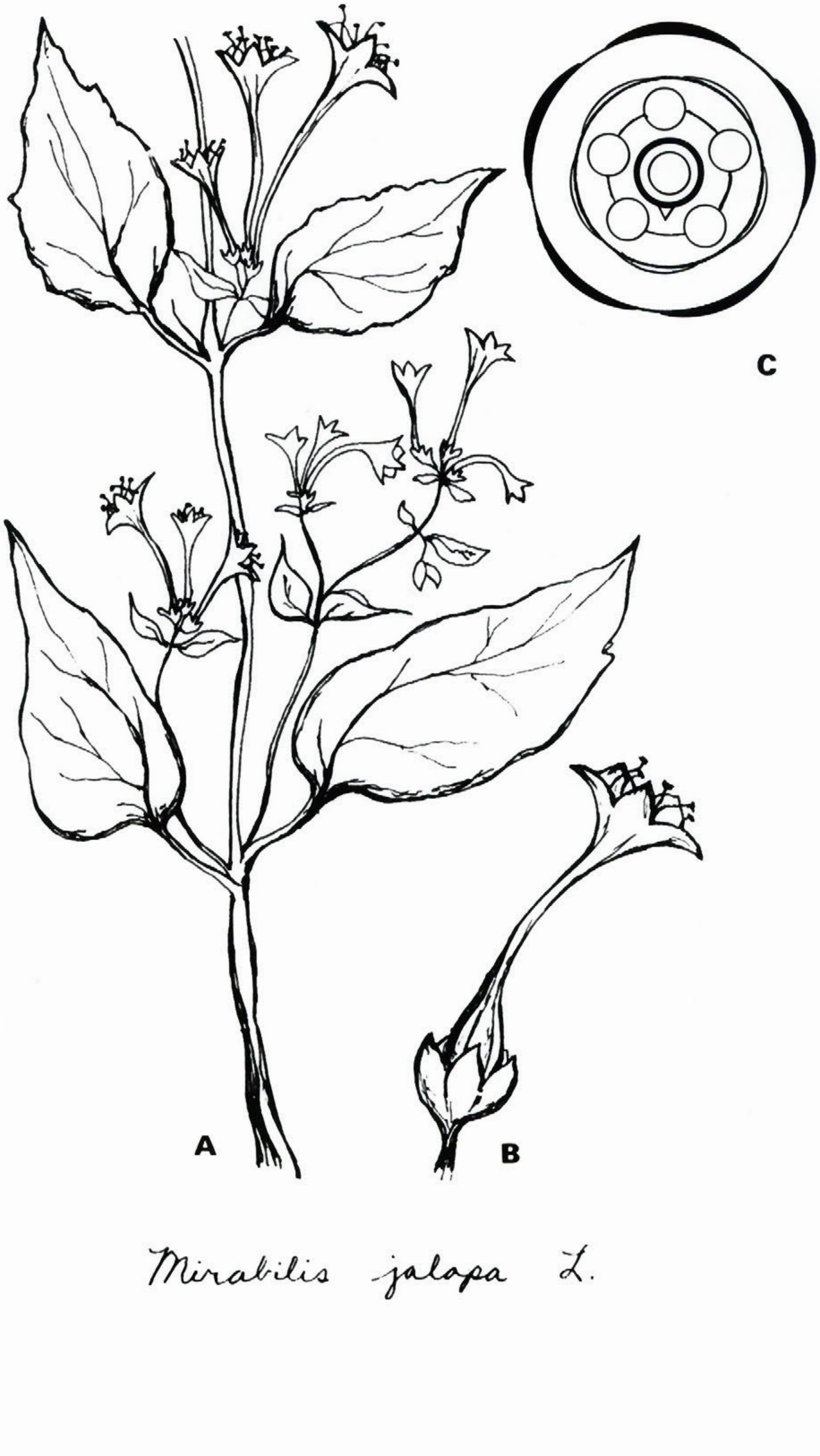

O
A
O
B
C
A
D
A
A
A
E
F

FIGURE IV

A. Sketch of the growth habit of <u>Mirabilis</u> during inflorescence production.

B. Detail of one mature flower.

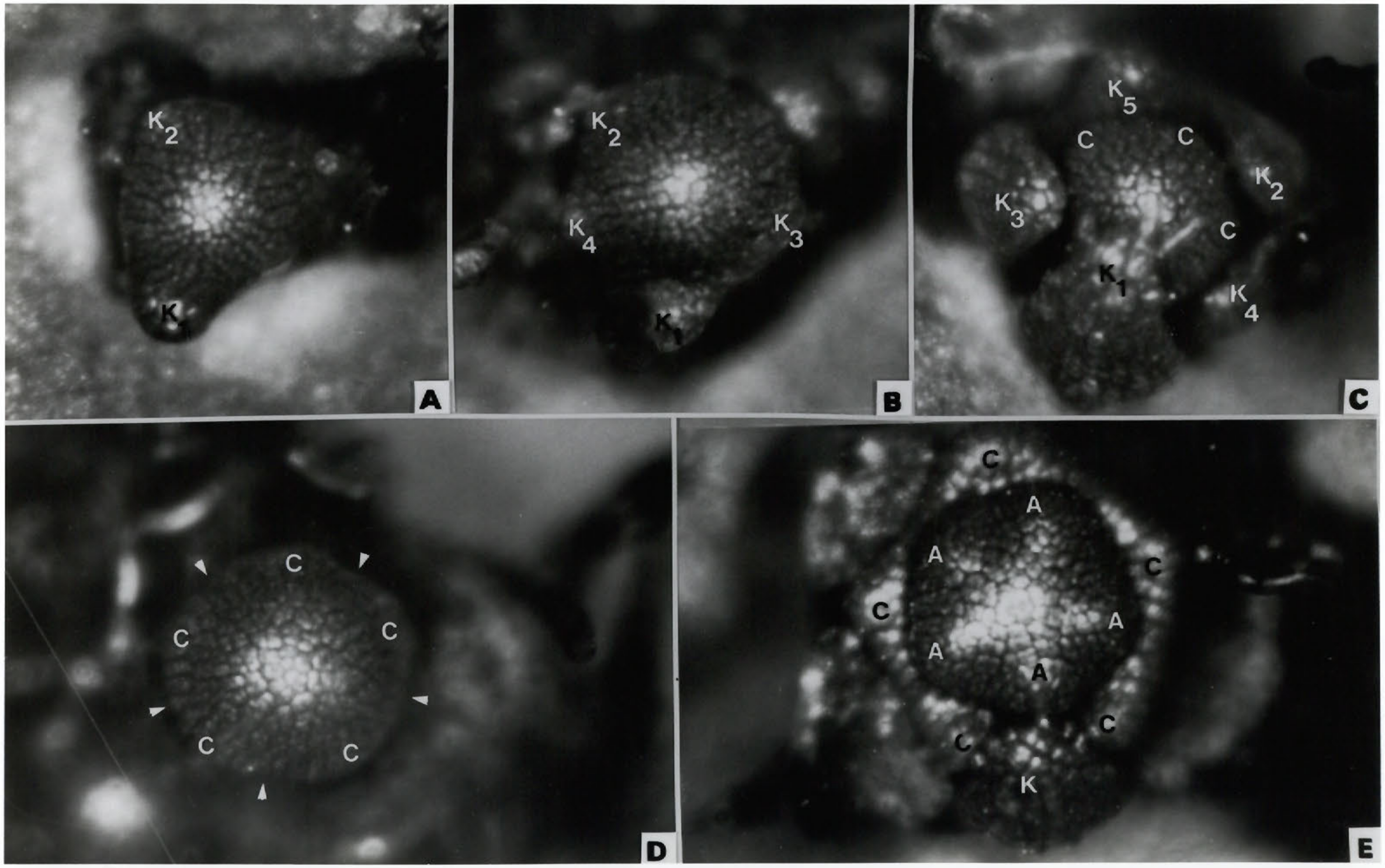
C. Floral diagram.



Mirabilis jalapa L.

PLATE XI. FIGURES A-E

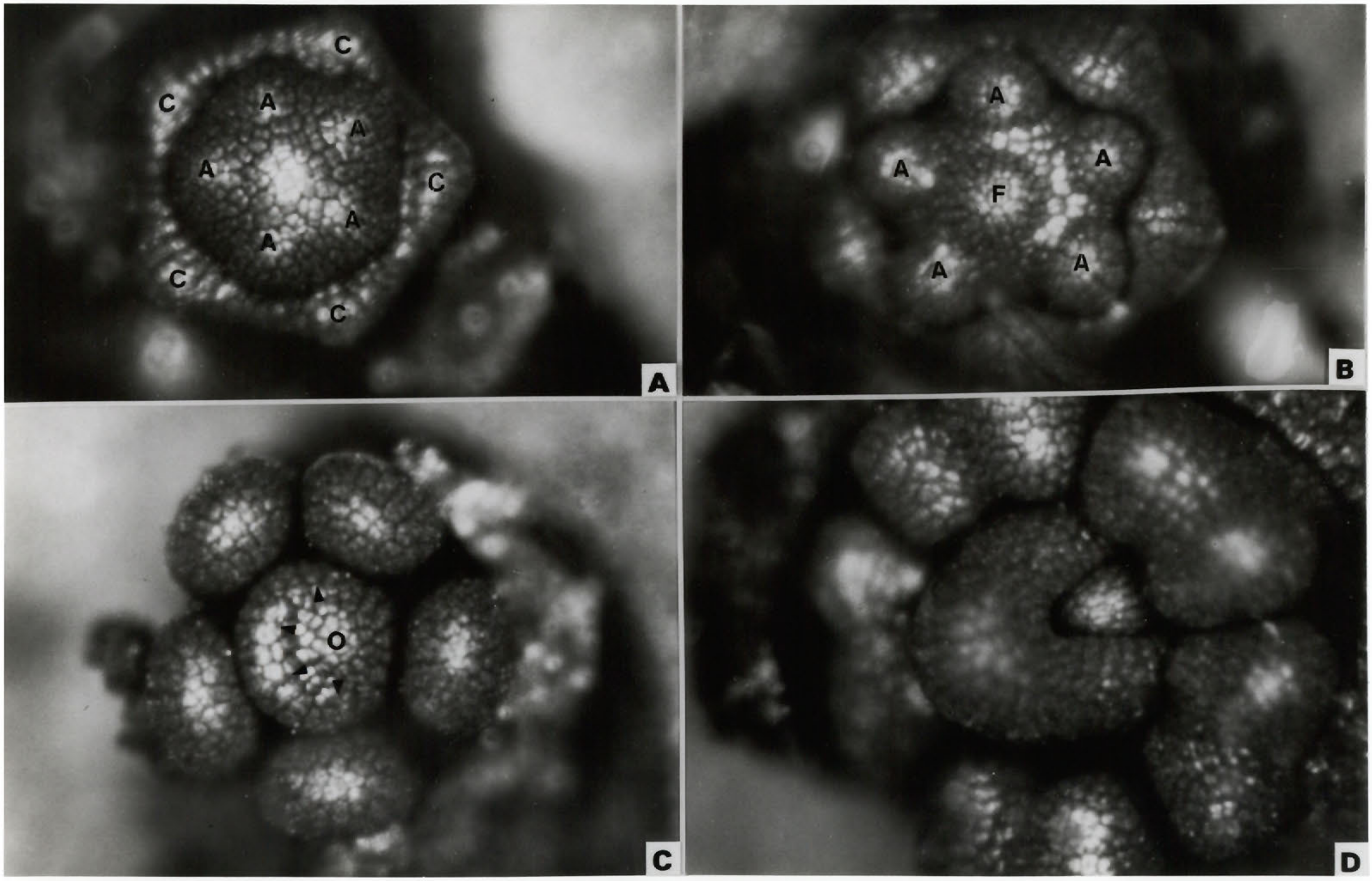
Figs. A-E	Top views of floral buds at successively older stages of development. X266
Figs. A-C	Sequential sepal (K) initiation. The primordia are numbered in their order of appearance. X266
Fig. D	The sepals have been removed to show the simultaneous initiation of the five petal (C) primordia. At this stage, growth between the petal primordia can already be seen (arrows) which will eventually produce the very long corolla tube. X266
Fig. E	An older floral bud showing the development of the corolla tube and the simultaneous initiation of the five stamen primordia (A) alternate to the petals. Note that one sepal has not been removed.



K_2
K_1
A
K_2
K_4
K_3
K_1
B
K_5
C
C
K_3
K_2
C
K_1
K_4
C
C
C
C
C
C
D
C
A
A
C
C
A
A
A
C
C
K
E

PLATE XII. FIGURES A-D

Figs. A-D	Top views of floral buds at successively older stages of development than those seen in Plate XI. X266
Figs. A,B	Further development of the corolla tube and stamen primordia. Enlargement of the floral apex in Fig. B. X266
Fig. C	The corolla has been removed to show the developing stamens and gynoecium. Growth is occurring in a semi-circular zone around the periphery of the floral apex to produce the gynoecial wall (arrows). The ovule (O) is initiated in a terminal and basal position in the centre of the gynoecial cavity. X266
Fig. D	A well developed floral bud showing the growth of the dorsal side of the gynoecium upwards to form what will eventually be a long style. The gynoecial walls are beginning to close around the terminal ovule. X266


C
C
A
A
A
C
A
A
C
C
A
A
A
A
F
A
A
B
O
C
D