

Comparative Analysis of Ovary Development  
in Selected Members of the Subtribe Abutilinae (Malvaceae)

by

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## Chapter I

### INTRODUCTION

Acting as the reproductive organ of angiosperms, the flower is under considerable selective pressure. Among the flowering plants, this structure represents an essential feature which unifies the group. Consequently the use of comparative floral morphology has been of considerable importance in delimiting evolutionary affinities of its members.

The gynoecium, or "female" portion of the flower, is no exception, for this is the part which bears the features that ultimately define the angiosperms. The gynoecium assumes a considerable diversity of forms, the similarities and differences of which represent perhaps the most important source of information in the phylogenetic ordering of plant groups.

The discipline of ontogenetic study is concerned with patterns of initiation and development of various parts and organs. Evolutionary changes, although manifested in mature structures, are a result of hereditary modifications in ontogenetic processes (Cusick, 1966; Takhtajan, 1972; Sattler, 1974; Gould, 1977). As such, phyletic information (although perhaps obscured) must reside in the development of

individuals. Ontogenetic studies, then, not only expand the data base of morphological descriptions but have a propensity for providing important insights into the homologies and derivations of certain structures.

The focus of this research was aimed at employing this potentially revealing approach in order to better understand various phylogenetically important gynoecial constructions. The Malvaceae was selected because of its diversity of gynoecial forms and the important role these have had in the systematics of the group (Kearney, 1951; Bates, 1968). Within this family, the subtribe *Abutilinae* was concentrated upon as it represented a more manageable size yet still contained examples of a wide range of gynoecial forms.

Three species were ultimately selected for study. These included *Abutilon Theophrasti* Medic., *Abutilon demissum* Fryxell and *Malacothamnus fasciculatus* (Nutt.) Greene. Between them they reflect a diversity of gynoecial conditions found throughout the group. These taxa, then, were considered in a comparative manner with respect to their gynoecial ontogeny in order to 1) better understand the morphological structure of the ovary, 2) evaluate the use of gynoecial characters in Malvaceae systematics and 3) potentially contribute important new data to the taxonomy of this family.

## Chapter II

### BACKGROUND

By design, the scope of this research has been a multidisciplinary one. A morphologically and phylogenetically important structure (the gynoecium) was carefully studied with respect to its development. Species selection and subsequent analysis of results were conducted within the taxonomic framework of the Malvaceae. The various disciplines involved here are given special attention to better orient the reader as to the nature of the project; elucidating current concepts, potential applications and associated controversies.

#### GYNOECIAL MORPHOLOGY:

Because of both its wide variation in form and its evolutionary significance, the "female" portion of the flower has received much attention and been the subject of as much controversy. As the morphological interpretation of the gynoecium can influence the way one perceives its ontogeny and this, in turn, has direct bearing on this research, it becomes necessary to briefly review the construction of the ovary and the controversial theories surrounding it.

Despite its many modifications, the gynoecium can often be recognized as a composite structure consisting of ovule-bearing subunits known as carpels. This latter structure has, consequently, been the center of much attention. In conjunction with its position and repetitive nature within the the gynoecium, the carpel is often considered to represent an appendage of the flower similar to that of a single stamen, petal or sepal. Extensive literature exists which considers the morphological nature and potential homologies of these structures. Much of this has been comprehensively reviewed by Eames (1961), Melville (1962), Lorch (1963), Esau (1965), and Meeuse (1965).

The term carpel is attributed to the greek word "carpon" which means fruit, but this association is actually an indirect one. More straightforwardly, it has its origin in the french word "carpelle", a diminutive of carpon and thereby implying fruitlet (Lorch, 1963). De Candolle is often attributed to having made the first usage of the word in the second edition of his "Theorie Elementaire" published in 1819 but, by this time, its concept was already well founded in scientific thought (Lorch, 1963). Robert Brown in 1816 understood well the fundamental nature of the carpel, defining the basic unit of the gynoecium as a "polyspermous legumen or folliculus whose seeds are disposed in a double series..." (in Lorch, 1963, p.

274). Brown's contribution, however, did not end here as he went on to explain the many modifications, "...abstractions, confluence, abortions and obliterations...", which can occur to obscure their delimitation (op. cit., p. 275). He proposed that the single-seeded achene of the Compositae was in fact a compound structure of two fundamental parts. We find, then, that from the inception of the term "carpel", and even before, the nature of the gynoecium as consisting of fundamental subunits which have undergone varying degrees of modification was well understood.

Where then lies the controversy? Although there has been some agreement regarding its existence, there persists considerable debate as to the carpel's evolutionary origin. Perhaps the oldest and certainly most popular theory concerning the homology of the carpel is that of the classical interpretation of the flower, first proposed by Goethe (1790) in his *Theory of Metamorphosis* (Wardlaw, 1968). Here, the axis of the flower is homologized with that of a determinate shoot and its appendages with that of leaves. The carpel, then, is considered to be derived from a fertile leaf, or sporophyll, whose margins have become inrolled to enclose the seeds.

Despite the wide acceptance of the "classical" theory, there exist a number of gynoecial conditions that are not

easily explained, such as the inferior ovary, basal ovule, and gynobasic style (Saunders, 1930; Meeuse, 1965). The inadequacies of the "classical" interpretation have led to the contrivance of a number of other divergent theories. Wilson (1942) suggested that the fertile appendages of the flower are derived from branch systems with terminal sporangia (telomes). Melville (1962), on the other hand, proposes that carpels have originated from fertile branches born on leaf-like structures (gonophylls). Troll (1939) and Leinfellner (1950) consider the carpel as homologous with that of certain more or less specialized leaves (from Esau, 1965). Takhtajan (1972) proposes that the flower may be a "neotenic variant" of a primitive strobilus, considering the carpels of primitive flowering plants to have a "very clearly expressed infantile appearance".

Some morphologists take an altogether different view. Saunders (1930, 1936) interpreted the syncarpous ovary to contain two whorls of polymorphic carpels, the outer being sterile and the inner fertile. Meeuse (1965) believed that the angiosperm carpel was polyphyletic. Still others (Thompson, 1935; Sattler, 1974) suggest that some gynoecia lack carpels altogether.

That the origin and construction of the carpel has not been

adequately explained is evidenced by the wide array of conflicting theories. That which bothers some comparative morphologists the most, and has the greatest bearing on this research, is the influence philosophical presuppositions have had on the reporting of empirical results. Lorch (1963) makes a distinction between "exposed" and "imposed" morphology as it relates to the delimitation of carpels. The former he defines as that which is amenable to direct observation whereas the latter is attributable to gynoecia where boundaries are obscure or non-existent.

In many cases "imposed" morphology has been just that, with investigators drawing dashed (imaginary) lines to "recover" carpels from gynoecia in which there is no observable demarcation (Sattler, 1974). Furthermore, such delimitations are often made with regard to the author's own conception concerning the nature of the carpel (e.g., Saunders, 1930, 1936). The inferior ovary represents a type of gynoecial construction which is not easily accommodated with respect to the "classical" theory of the carpel. Rao (1968) remarks that in many inferior ovaries whose condition has been attributed to the adnation of parts (i.e., sepals, petals and stamens), wall thickness often consists of no more than 5 or 6 cells. He finds the implication that tissues of at least a sepal, stamen and carpel are contained therein, a difficult one to accept.

Sattler (1974) also challenges popular theories concerning the origin of the inferior ovary, stating that "there is, of course, no developmental evidence for this interpretation". He does not necessarily reject the plausible notion that sepals, petals, stamens and carpels have become evolutionarily fused to form a compound structure but rather feels that there is insufficient empirical evidence to persuade him. The fact that such an hypothesis conforms well to the "classical" theory holds little weight.

What importance, then, does the controversy surrounding the carpel have to do with this project? Although the gynoecea of the Malvaceae do not pose as complex a problem as that of the inferior ovary, they do contain features which may be construed as incongruous with traditional concepts. What significance these may have will be considered at the appropriate time. Reporting such observations, however, is made difficult, since the pitfalls outlined by Lorch and Sattler are not easily avoided. Here, every attempt will be made to record results in as objective a manner as possible.

#### GYNOECIAL ONTOGENY:

In the following section a review is given of some of the basic developmental processes involved with the flower in

general and the gynoecium more specifically. This is then followed with several examples to illustrate the extent to which ontogenetic evidence can be applied.

During the transition from vegetative growth to flowering the floral apex generally undergoes considerable change in size and shape. The appearance of each floral appendage (sepal, petal, etc.) usually begins as a meristematic growth center in the form of a hemispherical bulge known as the primordium. The inception of primordia generally moves in a centripetal direction across the floral apex, beginning with the sepals and ending with the gynoecium.

The gynoecium often begins its development in the form of its constituent parts - the carpels. As with other appendages, the carpels generally make their first appearance in the form of primordia. In accordance with the classical interpretation of the flower, one might expect the carpels to initiate and develop much in the same way as leaves, and in many cases they do.

A number of ontogenetic processes exist which act to modify and differentiate the developing gynoecium. Their characterization and classification has been attempted by several investigators, including Sattler (1974, 1978) and

Takhtajan (1972). Of these, two will prove to be of special importance in this work and are considered here. They are 1) the coalescence or fusion of parts, and 2) their subsequent separation or dehiscence.

As noted earlier, the gynoecium assumes a great diversity of forms throughout the flowering plants. In some, the carpels remain free from one another and represent the condition known as apocarpy. In most angiosperms, however, the carpels are found to be continuous ("fused") with one another at the time of flowering. In these, the gynoecia are referred to as syncarpous. From a developmental perspective, the apocarpous construction is easily attained as carpels are generally initiated as free structures (carpel primordia) and require only their continued, independent growth. How then is the syncarpous condition achieved?

According to the classical theory, syncarpous gynoecia were the result of evolutionary fusion of carpels to one another. One might expect, then, for this to be reflected in their ontogenies, with carpels being initiated as free structures and later fusing to one another in the course of development. This, indeed, does happen, but we find that it is not the only way in which flowering plants realize syncarpy. Two basic ontogenetic processes are usually responsible. Their

existence has been known for some time, and they were originally termed postgenital and congenital fusions (Payer, 1857). In the former, appendages initiate and develop as free entities, secondarily fusing to one another (postgenitally) to form a compound structure. The latter, on the other hand, is marked by a continuity of appendages through zonal growth of an intercalary meristem beneath the bases of their primordia, i.e. they are "born" together, and hence the term "congenital". Figure 1 illustrates the way these two basic ontogenetic patterns can act to produce a similar structure.

These two developmental processes would appear to be clearly defined. Much controversy exists, however, particularly in regard to congenital fusion (Cusick, 1966; Sattler, 1974, 1978; Barabe and Vieth, 1979). The term "fusion" gives many students of floral ontogeny difficulty, for, in the case of congenital fusion, the developmental coalescence of surfaces is not actually observed. This conflict could seemingly be resolved by the replacement of the term congenital with "phylogenetic" for there are often good grounds, based on comparative morphology, for concluding that a unified structure has evolved from one with separate members (Cusick, 1966). Sattler (1978) and Barabe and Vieth (1979), however, argue that the concepts of phylogenetic and congenital fusion are not one and the same, as all ontogenetic

processes have a basis in phylogeny. The problem, then, is much like that of the delimitation of carpels mentioned earlier. Phylogenetic fusion (and any other theoretical fusion) is not an observable phenomenon. Although perhaps well founded, such concepts must always be carefully distinguished from empirical data.

Finally, just as "fusionary" processes are significant in their preparation for anthesis, so is dehiscence an important phenomenon in the subsequent maturation of gynoecia that form dry fruits or capsules. The position and manner in which dehiscence can occur differs widely. For most, separation occurs either between carpels (septicidal dehiscence) or along their dorsal walls (loculicidal dehiscence). The ontogeny of loculicidal dehiscence is generally characterized by the development of a suture zone, an outwardly visible groove which marks an area of structural weakness. This is often followed by dissolution of middle lamellae in a highly localized region to effect dehiscence (Addicott, 1982). With respect to septicidal dehiscence, investigators often presume that separation occurs between the surfaces of contact of adjacent carpels where there has been an incomplete fusion, ie. a simple "loosening" of appressed cell walls (Eames and McDaniels, 1947; Addicott, 1982).

In the species studied, we find the occurrence of both septicial and loculicial dehiscence. As with other groups, the mode and extent of dehiscence plays an important role in their phylogenetic classification.

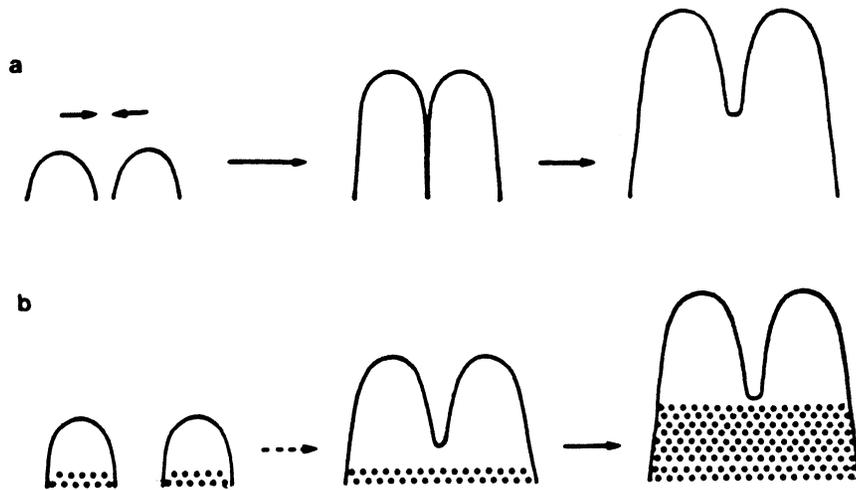


Figure 1: Two basic ontogenetic processes leading to the production of a compound structure; a) developmental coalescence of free surfaces or "post-genital fusion", b) continuity of appendages through an intercalary meristem (dotted) or "congenital fusion". (From Sattler, 1978.)

## ONTOGENETIC APPLICATIONS:

The field of developmental morphology takes on an exciting, new dimension when attempts are made to employ the data in the search for phylogenetic "clues". The application of floral ontogeny has generally been to discern the nature or homology of highly modified or reduced structures. From the viewpoint of the systematist, however, considerable potential should exist for the characterization and classification of taxa through the comparative analysis of developmental patterns. Examples of the this latter form of application are quite rare.

As mentioned earlier, the notion that early floral stages may reveal important insights is not new. Gould (1978) and others have continued to point out the obvious, that evolution works at the level of developmental processes. The significance of this concept is well illustrated by the following two examples.

Digitalis purpurea L. (Scrophulariaceae) contains a five-parted calyx and corolla, yet only four stamens. Singh (1979) found, through developmental analysis, evidence for a fifth stamen whose growth is arrested at an early stage and is therefore not present in the mature flower. This is significant as stamen number and position are given

considerable emphasis in angiosperm systematics.

The typical flower of Potamogeton consists of four tepals inserted on stamen connectives. This unusual position has led to the popular assertion that the tepals represent "outgrowths" and are stamen derived. Developmental work by Sattler (1965), however, shows that tepal primordia originate prior to and separate from the stamen primordia. Subsequent interprimordial growth results in the familiar adult form with tepals inserted on stamens. The notion that the tepals represent an "expanded sepaloid connective", therefore, is shown to be an incorrect presumption in light of the ontogenetic evidence.

The works of Singh and Sattler are but two examples of many which have helped to elucidate the interpretation of the primitive state or homology of an organ. The approach which is of greatest interest in this project, though, is that of the comparative analysis of developmental data. Sattler (1973) considered work in this area to be severely lacking and attempted to "fill the void" with his photographic atlas of floral organogenesis for some fifty species of plants. He did not, however, restrict himself to any particular group. The work of Ross (1982) is a good example of the seldom used approach where studies of floral ontogeny are employed within a

systematic framework. Here, flowers of five genera representing the three tribes of the Cactaceae were studied developmentally. They were found to differ with respect to 1) the time of cessation in the growth of the floral apex, and 2) the time of activation of an intercalary ring meristem within the receptacle. Ross was able to correlate these differences with established phylogenetic views of the family and, conversely, provide insight into the controversial position of the genus Epiphyllum.

#### TAXONOMIC FRAMEWORK:

The three species considered in this project were selected and analyzed within a taxonomic framework. The family Malvaceae was chosen because of its gynoecial diversity and the role these differences play in the classification of the group. In the following section family characteristics and subfamilial classifications are considered. Finally, the species selected are discussed.

The Malvaceae is a rather large family, consisting of some 1000-1500 species and more than 80 genera. The group is worldwide in distribution but reaches its greatest diversity in the dry sub-tropics of the New World. The family is perhaps

best known for its many showy flowers, a number of which have been grown as ornamentals (e.g., Hibiscus, Althaea and Abutilon species). By far its most important member is Gossypium, the seed hairs of which are used in the manufacture of cotton.

The Malvaceae is commonly referred to as a very natural group, exhibiting a high degree of uniformity for many of their characteristic features (Edlin, 1935; Bates, 1968). Almost all species are beset with stellate hairs and contain mucilage in either cavities or canals. Their leaves are alternate and most often simple. Lobing when present is, with few exceptions, palmate. The flowers of the Malvaceae are perfect, hypogynous and regular. The sepals and petals are distinct and typically number five. Perhaps the most conspicuous feature of the group is that of the androecium, which is represented by the connation of its many filaments into a monodelphous tube. The gynoecium consists of 2-many carpels (often a multiple of five) "fused" to form a compound structure. The ovules vary from 1-many per carpel and generally have an axile pattern of insertion. The fruit forms either a loculicidal capsule, schizocarp or, in many cases, a hybrid of the two. In some, the gynoecia mature into berries.

The family Malvaceae has historically been divided into

several tribes. Bentham (1862) distinguished four tribes: Malveae, Ureneae, Hibisceae and Bombacaceae. Schumman (1895), however, considered the genus Malope and its relatives to warrant tribal status and so removed them from the Malveae. More importantly, Schumman elevated the Bombacaceae to family status, a designation which has remained throughout more recent classifications. Edlin (1935) then transferred the tribe Hibisceae to the Bombacaceae in an attempt to delimit the Malvaceae as "a small and highly specialized family". Perhaps the most widely accepted breakdown of the family lies in Kearney's treatment. Here the Hibisceae are returned to the Malvaceae to provide a classification almost identical to that of Schumman's (Kearney 1951). More recently, new tribes have been segregated from the Hibisceae (Fryxell, 1968, 1975). For the purposes of illustrating the major features which delimit the subfamilial taxa, Kearney's classification has been adhered to and may be summarized as follows:

Tribe Malopeae: carpels numerous, occurring in 2 or more superposed whorls, 1 seed per carpel, ovule ascending, style branches of the same number as carpels, stigmas apical or decurrent, fruit a schizocarp.

Tribe Malveae: carpels in a single whorl, 1 or more

seeds per carpel, ovules ascending or pendulous, style branches of the same number as carpels, stigmas apical or decurrent, fruit a schizocarp or loculicidal capsule.

Tribe Ureneae: carpels in a single whorl, 1 seed per carpel, ovule ascending, style branches double the number of carpels, stigmas apical, fruit usually a schizocarp.

Tribe Hibisceae: carpels in a single whorl, usually numerous seeds per carpel, style branches of the same number as carpels or style undivided, stigmas apical, fruit a loculicidal capsule.

As with older tribal classifications, the breakdown proposed by Kearney is based exclusively on gynoecial characters. Of the various tribes, the Malveae represents the group of interest in this project as it is the largest and, structurally, most diverse. Due to its size and variation, this tribe is generally broken down into several subtribes. Although there are minor discrepancies among the various treatments, they are still basically in accord (Bates, 1968). The classification of Schumman recognizes three sub-tribes within the Malveae and is given here:

Subtribe Malvinae: Carpels in a single whorl, each carpel uniovulate, ovule ascending, stigmas introrsely decurrent on slender style branches, involucre bracts usually present.

Subtribe Sidinae: Carpels in a single whorl, each carpel uniovulate, ovule pendulous, stigmas apical (or decurrent), involucre bracts absent (except in some species of Sida).

Subtribe Abutilinae: Carpels in a single whorl, each carpel pluriovulate or uniovulate, uniovulate members with ascending ovules, stigmas apical (or nearly so), involucre bracts present or absent (generally present in uniovulate species).

As with the delimitation of tribes, subtribes of the Malveae are distinguished primarily on the basis of gynoecial characters. Of these, the Abutilinae is the taxon of interest in this project, because of 1) the variation in gynoecial structure represented, 2) the importance this variation plays in the delimitation of taxa, and 3) the existing controversy concerning its taxonomy.

Three species from the Abutilinae were chosen for actual

study. These include: Abutilon Theophrasti Medic., Abutilon demissum Fryxell, and Malacothamnus fasciculatus (Nutt.) Greene. Between them, they reflect a diversity of gynoecial conditions found throughout the group. Most prominent among these taxa are the differences in carpel and ovule number. Both of these have played a significant role in subfamilial classifications.

Carpel number has figured heavily in early taxonomic treatments of the genus Abutilon (Fryxell, 1983). Two major subsections were originally recognized, the Oligocarpae (with 5-8 carpels) and the Polycarpae (with more than 8 carpels). Although more recent treatments have delimited many more infrageneric groups and the Oligocarpae has been extensively revised, Abutilon Theophrasti (10-15 carpels) and Abutilon demissum (5 carpels) reflect a difference in gynoecial construction of some importance. Malacothamnus fasciculatus, with its numerous carpels, was selected, in part, as a basis for comparison.

The number of ovules per carpel has had an even more important role in Malvaceae systematics, carrying considerable weight in the delimitation of tribes and subtribes. In more recent works, however, there has been a trend to deemphasize the significance of ovule number (Bates 1968). For this study,

species were selected that demonstrated both the uniovulate and pluriovulate conditions in an effort to better evaluate the importance of this character.

Finally, a species was included (Abutilon demissum) which possessed a very interesting and unique structure - the endoglossum. Although it can take several forms, the endoglossum generally exists as a horizontal partition which more or less completely divides the cavity of the carpel. Studied rather extensively by Hochreutiner (1920), it too has had an important role in the delimitation of taxa, particularly at the generic level (Kearney, 1951). Once again, however, there has been a trend to downgrade the importance originally given it, suggesting that the endoglossum is of polyphyletic origin within the Malvaceae (Bates, 1968; Fryxell, 1980).

Many aspects of gynoecial development were studied in the species considered by this project. The above mentioned characters, however, were given particular attention, especially with respect to the possible mechanisms that might exist to achieve these taxonomically important gynoecial variations.

DEVELOPMENTAL STUDIES IN THE MALVACEAE:

Several ontogenetic studies of the gynoecia of the Malvaceae exist. In most cases, species selection has not been relegated to a particular subfamilial taxon. Where members of the tribe Malveae have been considered, they have been selected almost exclusively from the subtribe Malvinae. None of these investigations have addressed species belonging to either Abutilon or Malacothamnus. A brief review of these works is provided here.

Duchartre (1845) conducted a study of floral development in a number of species of the Malvaceae in what represented, perhaps, the first endeavor to look at gynoecial ontogeny in this group. Although he managed to consider members from each of the tribes of the family, his work with the Malveae was restricted solely to the subtribe Malvinae. Nevertheless, a number of his observations are found to show important insights that are unreported by subsequent investigators.

Payer (1857) provided a comprehensive review of floral development throughout the angiosperms and, in so doing, investigated several species belonging to the Malvaceae. His observations sometimes contradict those of Duchartre, a fact which he was quick to acknowledge.

As noted earlier, Sattler (1973) also conducted a review of

floral development in the angiosperms. Here, he provided photographic evidence (a technique unavailable to Payer and Duchartre) for some fifty species of plants, two of which were from the Malvaceae. These included Malva neglecta Wallr. and Althaea rosea (L.) Cav., again both members of the subtribe Malvinae.

In his anatomical study of the gynoecium of Bakeridesia, Klotz (1975) considered some aspects of organogenesis but did not dwell much on it. His contribution has been important for this study, however, as Bakeridesia is a good member of the subtribe Abutilinae and his work provides histological data not found in other investigations.

Finally, van Heel (1978) addressed the nature of the pistil in members of the tribe Ureneae, where twice as many styles exist as there are carpels. Here again, good anatomical information is provided for comparison.

The works of the above mentioned investigators are revealing. The value of the existing data on gynoecial development in the Malvaceae, however, is better understood in light of the developmental descriptions of species studied in this project. For this reason, the actual findings of previous authors are considered later, as various ontogenetic processes

are discussed and evaluated.

Chapter III  
MATERIALS AND METHODS

Material used for this study was procured from several sources. Abutilon Theophrasti was collected on the VPI & SU campus, Blacksburg, Virginia on November 4, 1983. Collections of Abutilon demissum were made by Dr. Paul Fryxell while on a trip to the state of Guerrero, Mexico in the fall of 1982. Malacothamnus fasciculatus was procured from the University of California Botanical Garden in Berkeley, California on July 21, 1982. The original collection of the latter came from Santa Cruz Island, California.

With all three species, floral buds of various stages of development were taken from living material and immediately fixed in FAA (after Johansen, 1940). More mature buds were partially dissected to allow for better penetration of the fixative. After a minimum of 24 hours, material was washed and stored in 70% ethanol.

While immersed in ethanol, buds of various stages were dissected with the aid of a dissecting scope and razor blade chips to expose their gynoecia. Overall bud length was found to correlate fairly well with the relative maturity of the

gynoecia they contained. This was used to target floral buds for dissection but, ultimately, gynoecia were viewed directly to determine the suitability of the stages they represented.

Different concentrations of ethanol produced different properties for dissection. At too high a concentration the material became brittle, but some hardness in the tissue was desirable. A concentration of approximately 80% ethanol was found to be ideal. These dissections were then studied topologically and, when appropriate, supported by sectioned material.

Gynoecia were studied topologically with the use of scanning electron microscopy. Material was dehydrated through a graded series to absolute ethanol and prepared in a Ladd critical point dryer using liquid carbon dioxide. Dissections were then mounted on stubs and grounded with silver conducting paint. These were coated with gold in an SPI Sputter 12121 to a thickness of 200-300 angstroms. Specimens were viewed with a JEOL JSM-35C scanning microscope and photographed with Polaroid type 55 film. Larger specimens of Abutilon Theophrasti were photographed fresh under a Wild M5A dissecting scope equipped with a MPS 55 Photoautomat and 35 mm attachments. Selected specimens of each species were drawn to scale from photographs in order to better perceive the zonal

and radial growth that occurs.

Serial sections were made to compliment topological studies as needed. Originally, attempts were made to use paraffin embedded material. Properties associated with this group of plants, however, made this approach unfeasible. Stellate trichomes, common to all three species, are thick-walled and heavily lignified. They tend to resist the knife, fragment and tear through the tissue. In addition, mucilage (also found in all three) will diffuse from freshly sectioned material and obscure details if processed by standard paraffin methods. Alternatively, dissections were embedded in plastic resin, and this was found to give satisfactory results. Here, all extraneous tissue was removed and specimens were dehydrated through a graded series to absolute ethanol. Tissue was then infiltrated with propylene/resin over a minimum of 24 hours and embedded, using flat molds, in Poly/Bed 812 resin. Material was sectioned on a Porter-Blum MT-1 Ultra-microtome using glass knives. Sections were cut at 1-2  $\mu\text{m}$  in thickness, stained with 1% toluidine blue in 1% borax (as per Berlyn and Miksche, 1976) and photographed with a Leitz Ultraphot microscope fitted with a Nikon 35 mm photosystem.

In certain special cases it was desirable to section material originally used for S.E.M. study. This was done by

putting the critical point dried and gold coated specimen directly in propylene oxide and continuing with the infiltration series.

## Chapter IV

### DESCRIPTIONS

As discussed earlier, problems exist with the use of traditional terminology as it applies to developmental morphology, especially with regard to the gynoecium. For this reason, several terms that will be used in the descriptions to follow are, here, clearly defined.

The term "carpel" is applied to a fundamental unit of the gynoecium that bears and encloses one or more ovules. As carpels are clearly manifested in the mature gynoecia of the Malvaceae, use of the term is still quite appropriate despite certain deviations from traditional carpel theory.

"Zonal growth" is defined as a developmental process which results from meristematic activity over an extended area. Such meristematic regions sometimes exist in the form of a continuous ring and act to produce cylindrical structures, examples of which are to be found in the species studied.

"Fusion" here refers to an observable (developmental) event represented by the coalescence of two or more formerly free surfaces. Hence, "congenital fusion" is not a true fusion as defined but, as noted earlier, generally depicts some form of

zonal growth. The terms "postgenital" and "congenital" will not be used in the descriptions that follow.

#### DEVELOPMENT IN Abutilon Theophrasti:

The gynoecium of Abutilon Theophrasti is first discernable as a continuous ring (Fig. 3) which precedes the formation of any primordia. Regions of restricted growth on its inner flank result in the development of 10-15 "locular depressions" (Fig. 4) which ultimately correspond to the chambers of mature carpels. Radially oriented septa appear in alternate positions with the young locules (Fig. 5) and grow to form the lateral walls found between adjacent carpels.

The gynoecial ring continues to grow upwards, both externally and on the interior, such that a residual apex is defined (Fig. 6). This aspect of A. Theophrasti's gynoecial development is not so pronounced as the zonal growth which soon ensues from below. The longitudinal files of cells present in figures 7 and 8 (at "z") are evidence of the contribution of this meristematic activity.

Throughout early stages of development, considerable radial expansion also occurs (Fig. 2). This factor, coupled with the

contribution of zonal growth, helps to explain the way in which locular depressions expand within otherwise homogeneous tissue to form the chambers of mature carpels (Fig. 4-8).

We see then that the body of the gynoecium is a singular structure. During early stages of locule formation there is continuity throughout (Fig. 16). At later stages of development, when the lateral walls have become more clearly defined, there is still no perceptible evidence for the fusion of carpels to one another or to the residual apex (Fig. 17, 18). Even at anthesis, after the gynoecium has undergone considerable growth and differentiation, the shared lateral walls show complete uniformity (Fig. 22).

As the gynoecium approaches anthesis the dorsal walls of the carpels bulge outwards, adding to their increasing distinctness (Fig. 9). Just prior to the opening of the flower several secondary features of the gynoecium manifest themselves. Most prominent are the appearance of the many stellate trichomes and the development of the receptive, papillose cells on stigmatic surfaces (Fig. 10).

After flowering, the gynoecium enlarges considerably and becomes heavily lignified. As the fruit begins to dry, the carpels first split along their dorsal walls to effect

loculicidal dehiscence (Fig. 11). Eventually, the gynoecium develops septicidal dehiscence as well, the carpels disarticulating from one another to form mericarps (Fig. 12). The residual apex, portions of carpellary walls and remnant funiculi remain on the plant in a composite structure often referred to as the "columella" (Fig. 13).

The dehiscence patterns found in the fruits of Abutilon Theophrasti have their origin in tissue differentiation that begins just prior to anthesis. In figure 9, a faint groove can be detected forming along the backs of each carpel, marking the place of future dehiscence. Anatomically, this region of the carpel reveals two vascular bundles developing in close proximity to one another and forming the bulk of the dorsal midrib, excepting a very narrow band of parenchymatous cells (Fig. 23). A differential in tissue strength is thereby created such that any tensions generated by the drying of the fruit causes a separation of the parenchyma cells between the two bundles.

The disarticulation of carpels from one another is effected through a mechanism somewhat analagous to that of loculicidal dehiscence. Around the time of anthesis, surface layers of the lateral walls undergo periclinal divisions to produce a multiseriated epidermis (Fig. 22). As the fruit matures, this

epidermis transforms into a layer of heavily lignified, elongated fibers lining the interior of each carpel (Fig. 14). As with loculicidal dehiscence, a differential in tissue strength is developed across the lateral wall. During drying of the fruit tensions are presumably produced which cause the heavily reinforced, inner surfaces of the carpels to pull away from one another. The lateral wall ultimately "gives" throughout its homogeneous interior where the undifferentiated, parenchymatous cells are considerably weaker. That the dehisced surface of the schizocarp represents an uneven rupturing of thin-walled cells is evidenced by figure 15.

Ovules first appear at about the time that locules develop a clearly defined internal space (Fig. 6). Three ovule primordia are initiated per carpel in an acropetal sequence. The upper two are born laterally and alternate with the ventral suture (Fig. 17). The bottommost, however, originates in a central position directly beneath the suture (Fig. 18). Despite the temporal differences in inception, all three ovules have approached an equivalent stage of maturity when integumentary layers begin to make their first appearance (Fig. 8). Because of restrictions in space, the ovules become pushed into a "superposed" position as they mature. Points of attachment, however, still reflect their characteristic pattern of

initiation (Fig. 19, 20, 21).

Style primordia appear in conjunction with the onset of ovule primordia. They originate apically above each locule (Fig. 6) and grow upwards as free structures (Fig. 7). As they continue to elongate, however, their lower portions fuse to one another to form a compound structure in part (Fig. 9). As the flower approaches anthesis, active growth along the dorsal walls of the carpels causes an "overarching" of the style bases and their orientation towards a lateral position on the interior of the gynoecium (Fig. 8-10). Evidence for the fusion of free surfaces is still present in the gynoecium at anthesis (Fig. 24).

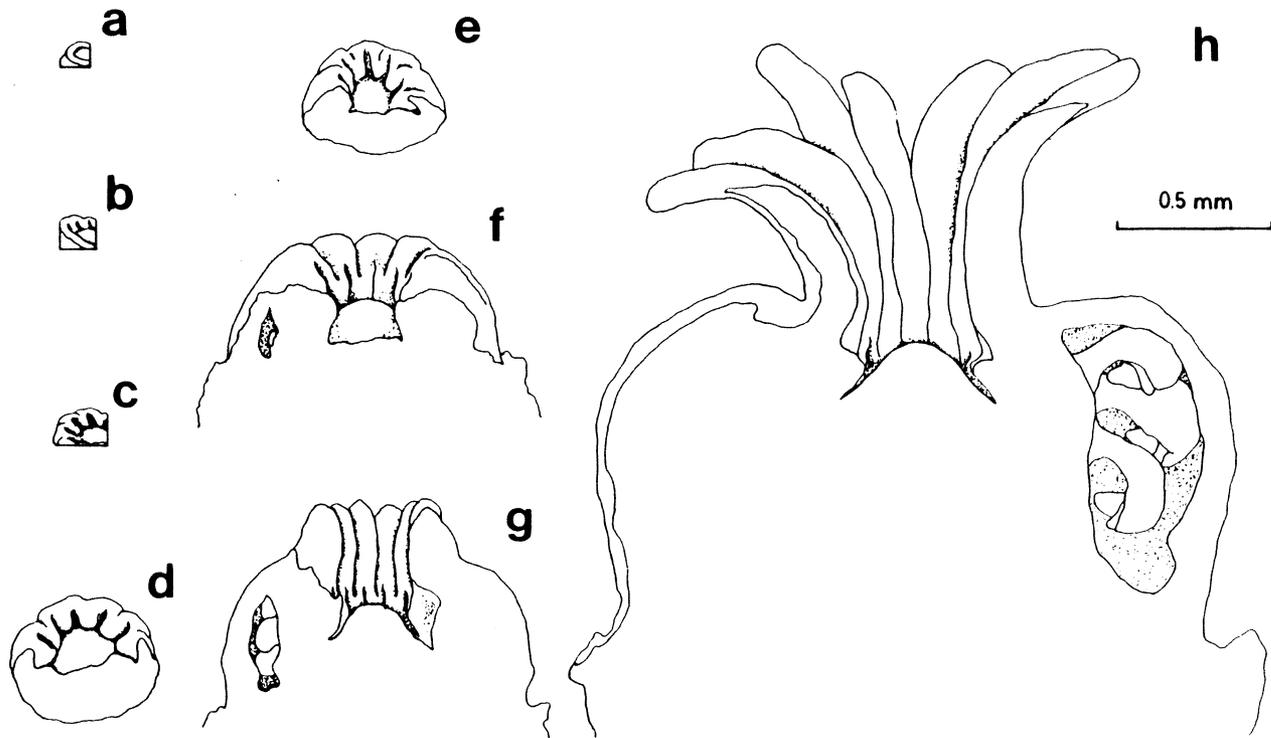


Figure 2. Developmental sequences of *Abutilon Theophrasti* drawn to same scale.

Fig. 3-8. Scanning electron micrographs of developing gynoecia of Abutilon Theophrasti.

3. Oblique view showing initiation of the gynoecial ring. x780.

4. Oblique view of gynoecial ring with locular depressions (arrow) initiated along its inner flank. x650.

5. Oblique view. Common lateral walls (lw) have become prominent. x430.

6. Side view with several carpels removed. Style (s) and ovule (o) primordia have been initiated. Residual apex (ra) is clearly defined. x80.

7. Cut away side view showing continued growth of styles and ovules. Zonal growth (z) is apparent. x80.

8. Cut away side view. Styles have elongated and have been oriented towards the interior of the gynoecium. Ovules are beginning to develop integumentary layers. Body of the gynoecium exhibits further zonal growth (z). x30.

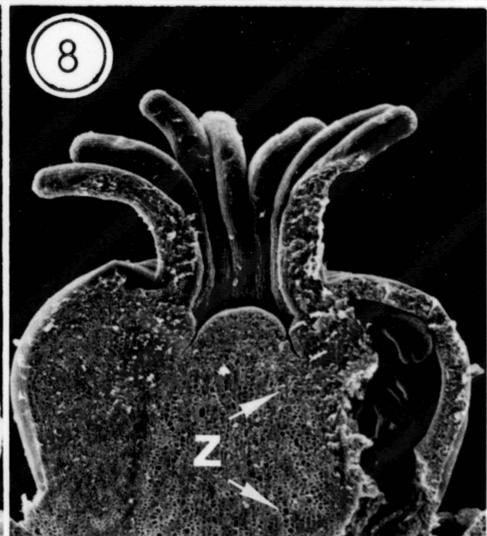
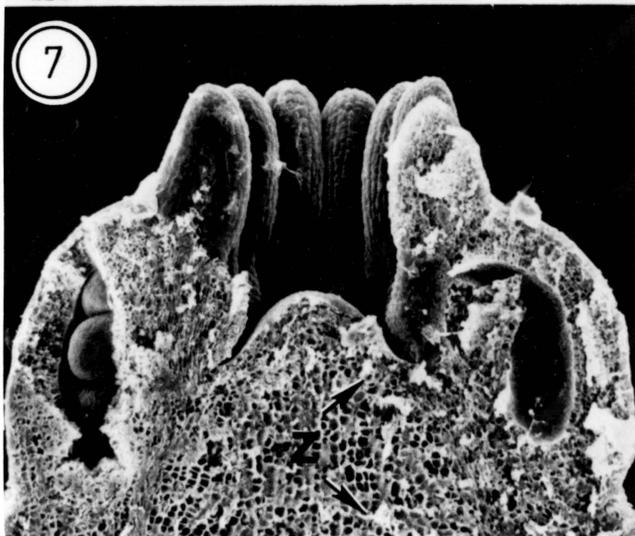
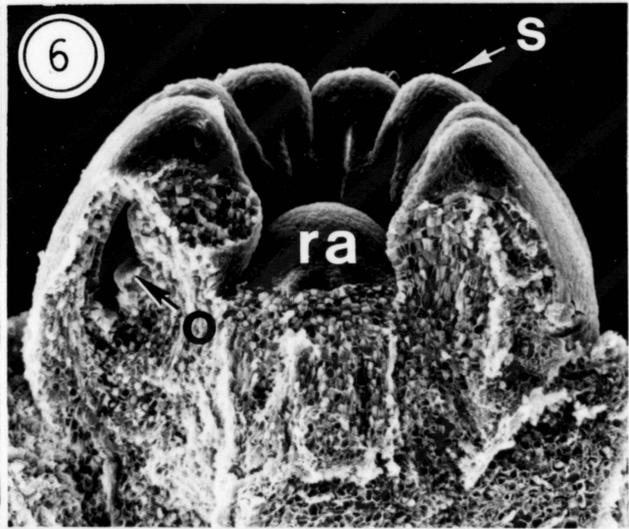
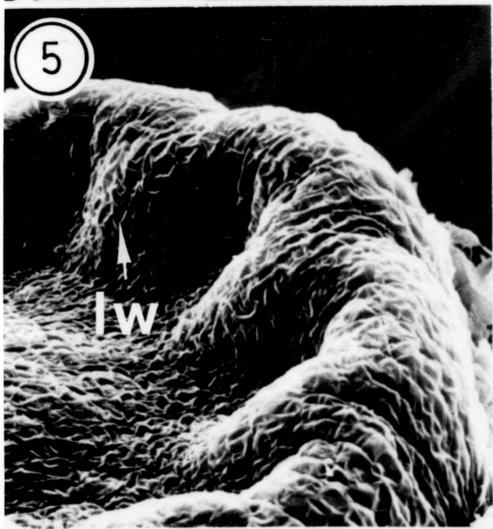
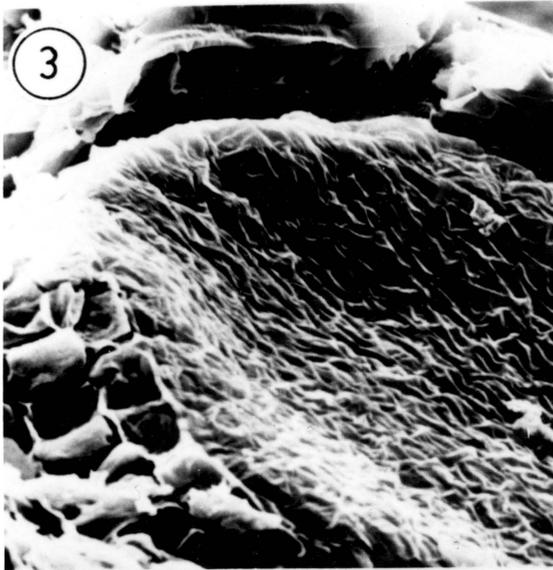


Fig. 9-13. Further development of the gynoecium of Abutilon Theophrasti.

9. Scanning electron micrograph showing prominent dorsal bulging. Locular grooves are present on the backs of carpels marking the regions of dehiscence. Styles are developmentally fusing to one another (arrow). x28.

10. Scanning electron micrograph of gynoecium at anthesis showing several secondary features of development. x17.

11. Side view of mature fruit. Loculicidal dehiscence has occurred. x3.

12. Disarticulated carpel. Arrows show area of septicidal dehiscence. x3.

13. Close-up of columella. Funiculi (f) and portions of the lateral walls (lw) still remain. x13.

Fig. 14-15. Scanning electron micrographs of surfaces of a disarticulated carpel of Abutilon Theophrasti.

14. Inner wall showing pattern of highly lignified fibers. x185.

15. Outer surface in the region of the septicidal dehiscence showing several layers of degraded parenchymatous cells. x200.

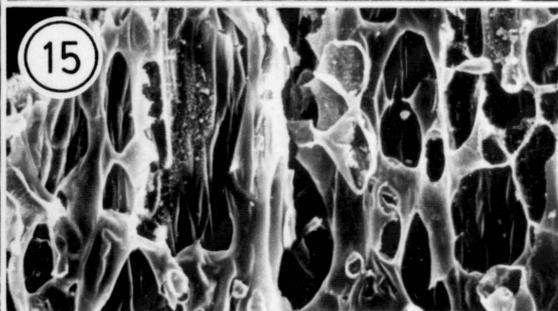
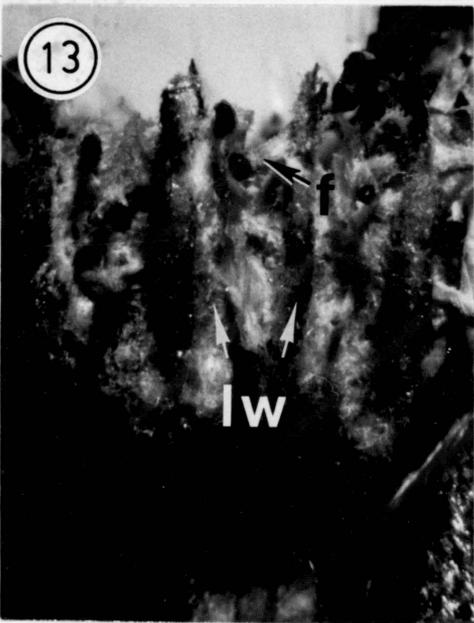
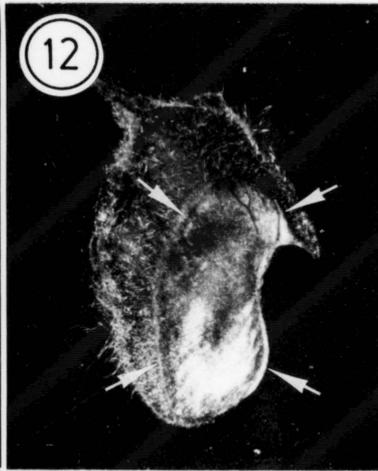
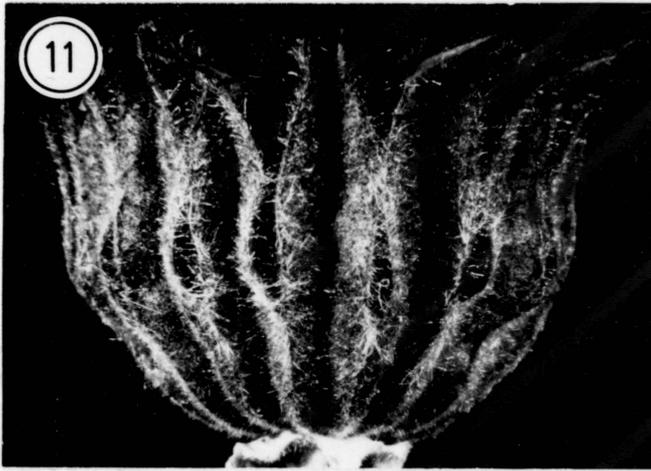
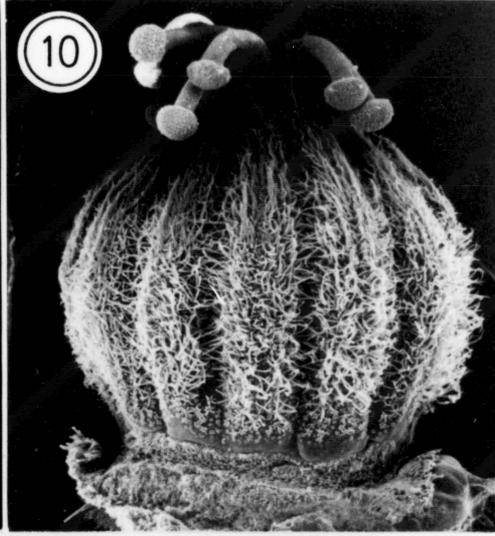
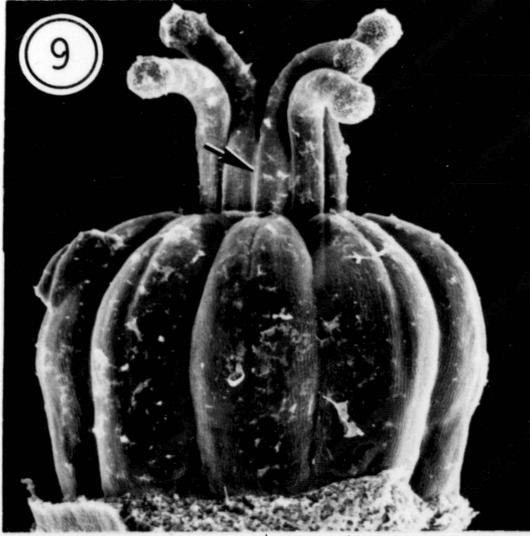


Fig. 16-24. Cross sections through the gynoecia of Abutilon Theophrasti.

16. Early stages of gynoecial development showing gynoecial ring (gr) with locular depressions (ld). x230.

17. Initiation of middle ovule primordium (o) in lateral position. Lateral wall (lw) continuous between adjacent carpels and with the residual apex (ra). x230.

18. Initiation of lower ovule primordium in a central position (arrow). x230.

19. Upper ovule insertion (f) at anthesis in a lateral position with respect to the ventral suture (s). x90.

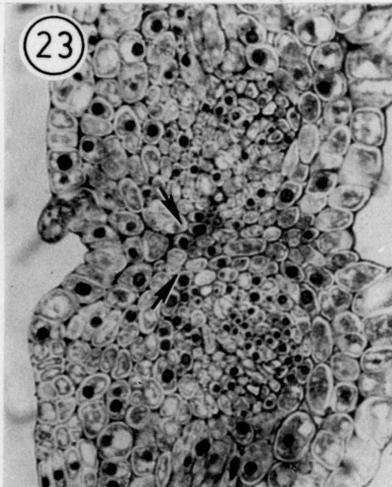
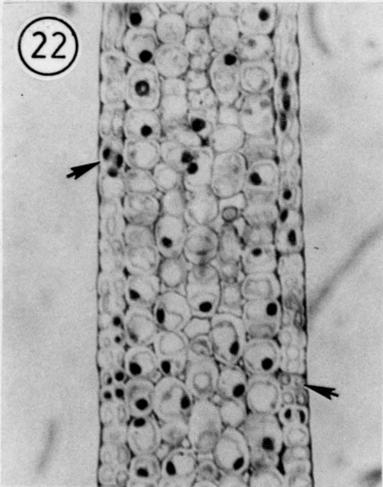
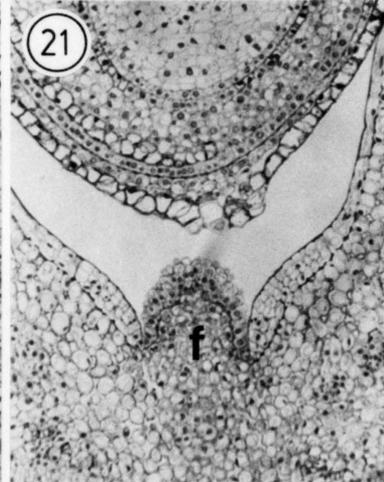
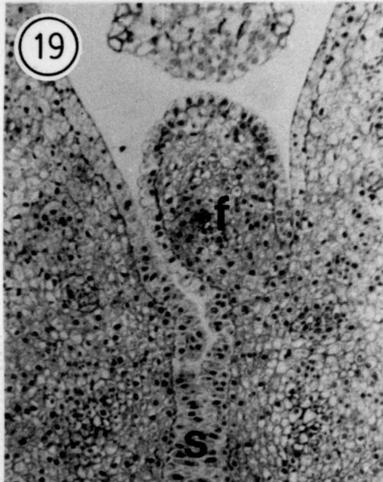
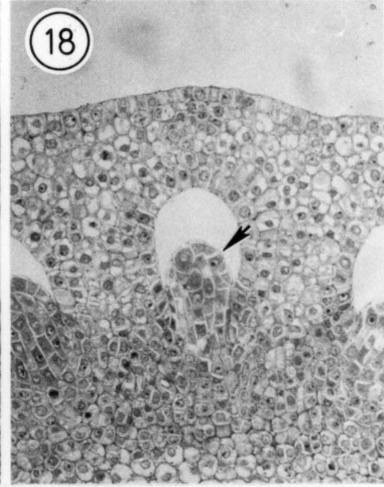
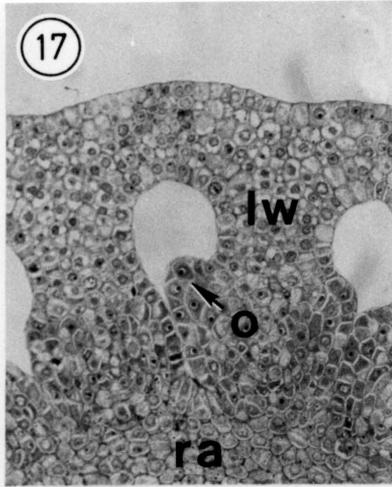
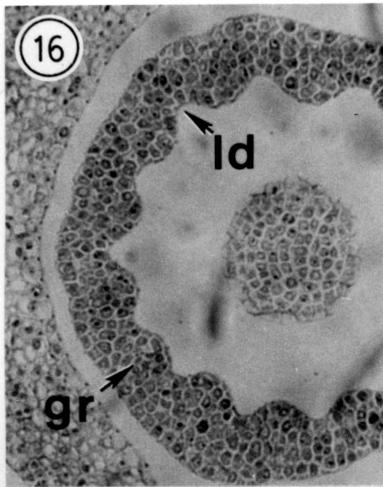
20. Middle ovule insertion (f) at anthesis in a lateral position with respect to the ventral suture (s). x90.

21. Lower ovule insertion (f) at anthesis born in a central position. x90

22. Common lateral wall at anthesis showing continuity and the development of a multiseriated epidermis (arrows). x230.

23. Dorsal suture at anthesis. Region of parenchymatous cells (arrows) marks place of future dehiscence. x230.

24. Close-up of a portion of the compound style. Arrows mark region of fusion of two stylar components. x230.



DEVELOPMENT IN Abutilon demissum:

Development of the gynoecium of Abutilon demissum shows many similarities with that of Abutilon Theophrasti. It originates first as a continuous ring prior to the formation of any primordia (Fig. 26). The region this ring delimits, however, is markedly smaller (Fig. 25a) and what may be referred to as a "residual apex" quickly becomes obscured (Fig. 29, 31).

Five locular depressions develop on the inner flank of the gynoecial ring (Fig. 27). These enlarge to form the carpel chambers (Fig. 28, 29, 31) through the processes of zonal growth and radial expansion (Fig. 25) noted earlier. As with Abutilon Theophrasti, the body of the gynoecium is a singular structure in which no fusionary processes have occurred. As the gynoecium matures, carpels become outwardly distinct through bulging of their dorsal walls and, just prior to anthesis, develop numerous stellate trichomes over their surfaces (Fig. 36, 37).

Although mature fruits of Abutilon demissum were not available for study, tissue differentiation at anthesis reflects patterns very similar to those found in Abutilon Theophrasti. Dorsal grooves along the backs of the carpels

exist at the time of flowering (Fig. 36) and anatomical evidence shows this region to contain two developing vascular bundles separated by a narrow zone of parenchymatous cells (Fig. 40). Likewise, cross sections of the lateral walls reveal a pronounced multiseriate epidermis (Fig. 39) which presumably plays a role in the septicidal dehiscence described by Fryxell (1980). These superficial and internal features strongly suggest modes of dehiscence similar to that of A. Theophrasti.

Three ovule primordia are initiated per carpel in an acropetal sequence. The bottommost ovule develops first and in a central position beneath the ventral suture (Fig. 30), whereas the upper two originate laterally and in alternate positions (Fig. 30, 32). Although ovule maturity is significantly different during early stages, they quickly attain an equivalent state by the time integumentary layers develop (Fig. 33, 34). By anthesis the ovules have become superposed upon one another (Fig. 36, 37) yet still reflect their pattern of initiation by the attachment of their funiculi (Fig. 41, 42, 43).

As with Abutilon Theophrasti, style primordia initiate above each locule at the time of appearance of the ovules (Fig. 29), grow upwards as free structures (Fig. 31, 32) and later

fuse throughout their lower regions to form a compound structure (Fig. 37, 44). Overarching by the dorsal walls is also found to occur. Consequently, style bases orient toward the interior of the gynoeceium (Fig. 33) and, by anthesis, have their insertion deep within the body of the ovary (Fig. 37).

Finally, Abutilon demissum is distinguished from the other two species studied by the possession of a partition within the chambers of the carpels known as the endoglossum. This structure first appears as a horizontal bulge on the interior of the dorsal wall (Fig. 33), which grows inward, between the lower and middle ovules, as a plate-like structure (Fig. 35). By anthesis the endoglossum completely occludes the bottommost ovule from the remainder of the cavity (Fig. 36, 37). That the endoglossum represents a simple ingrowth of the dorsal wall is supported by anatomical evidence that shows complete continuity of the epidermis and internal tissues (Fig. 38).

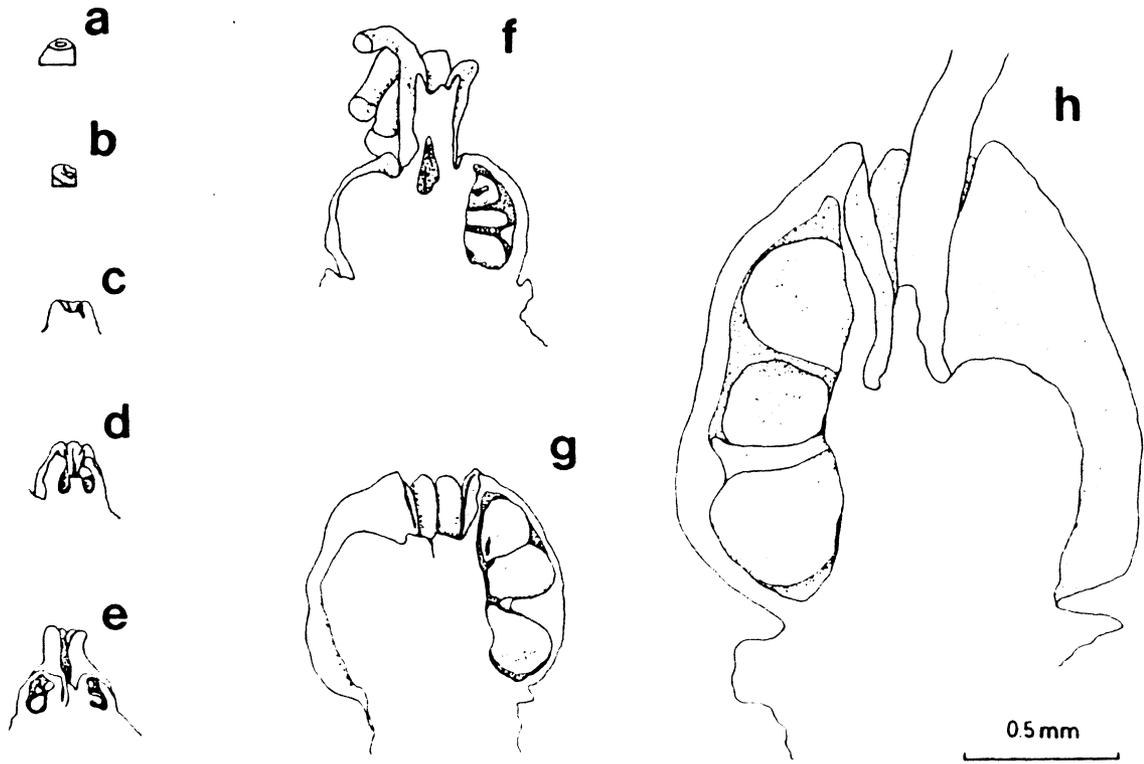


Figure 25. Developmental sequences of Abutilon demissum drawn to same scale.

Fig. 26-31. Scanning electron micrographs of gynoecial development in Abutilon demissum.

26. Oblique view showing initiation of gynoecial ring. x675.

27. Oblique view of gynoecial ring with locular depressions (arrow) initiated along its inner flank. x990.

28. Cut away side view showing development of common lateral walls (lw) and extent of young locule (l). x810.

29. Side view with two carpels removed. Style (s) and ovule primordia have been initiated. x240.

30. Close-up of fig. 29 showing ovule initiation. Lower ovule (o1) centrally positioned beneath ventral suture. Middle ovule primordium (o2) younger and laterally born. x720.

31. Cut away side view showing upward, free growth of styles (s) and further development of ovules. x180.

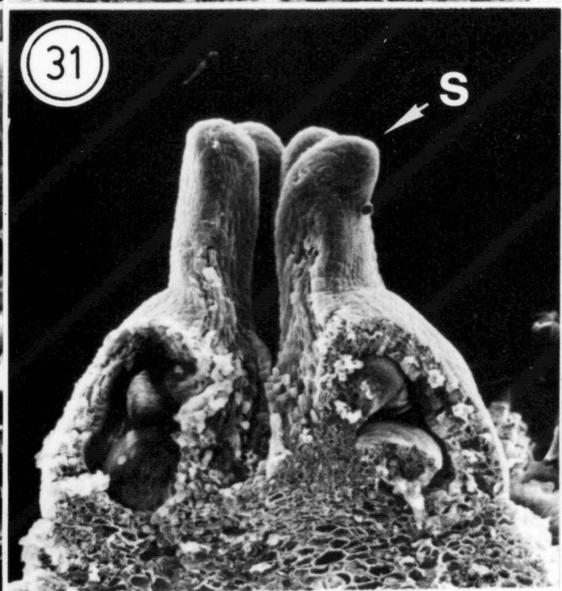
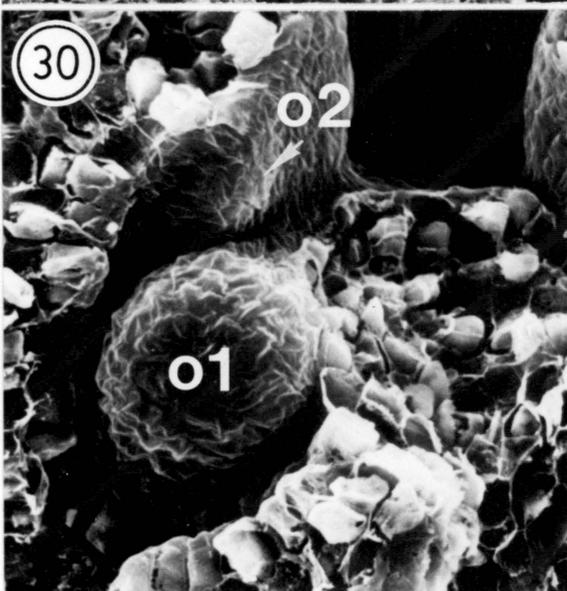
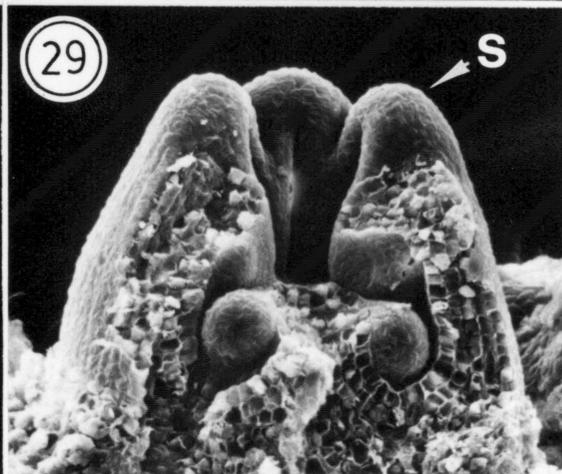
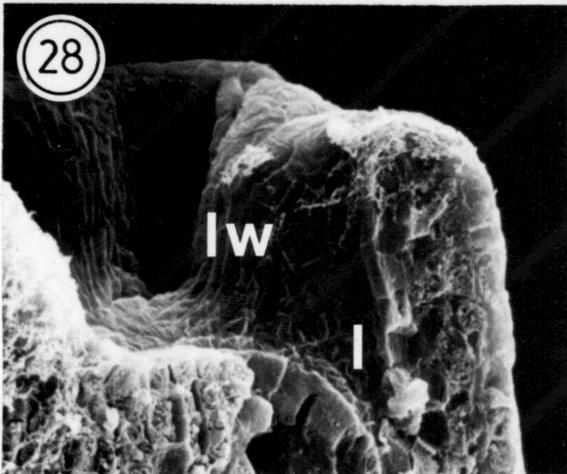
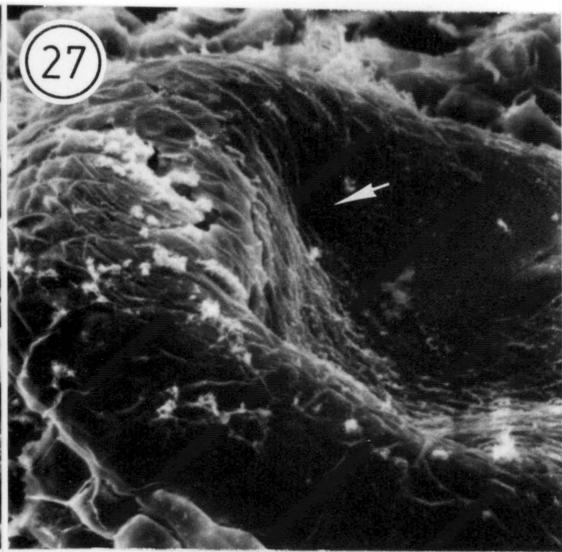
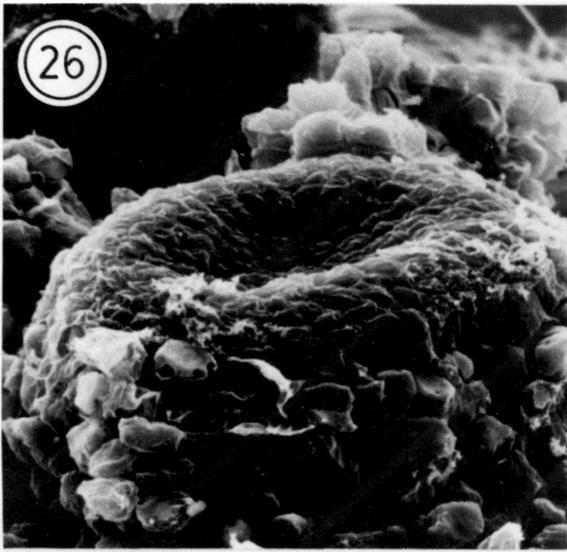


Fig. 32-37. Scanning electron micrographs of gynoecial development of Abutilon demissum.

32. Torn open carpel showing free growth of style (s), acropetal development of ovules and their positions (o). x240.

33. Cut away side view. Styles have begun to fuse to one another. Endoglossum (e) has been initiated. x80.

34. Close-up of upper ovule showing development of outer (oi) and inner (ii) integuments. x400.

35. Cut away side view (styles removed). Carpels have begun to overarch original insertion of styles. Endoglossum (e) protrudes farther into cavity. x60.

36. Side view at anthesis with contents of one carpel exposed. Dorsal bulging has occurred and ovules have been pushed into a superposed position. x43.

37. Cut away side view at anthesis. Endoglossum completely partitions locule. Carpels have extended far above the point of style insertion (arrow). x34.

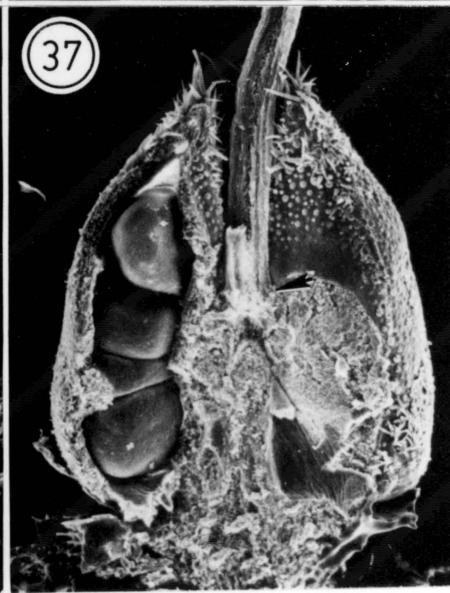
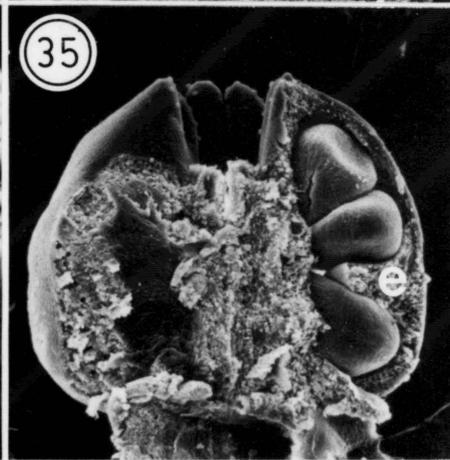
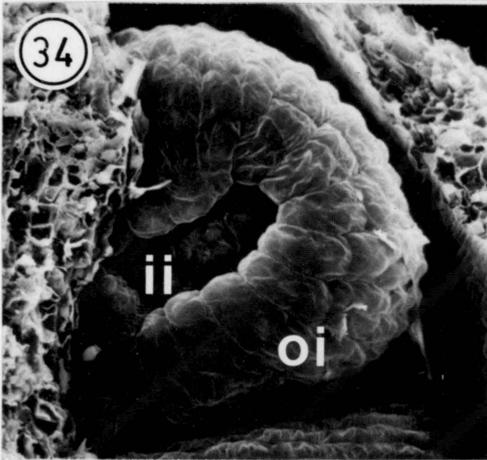
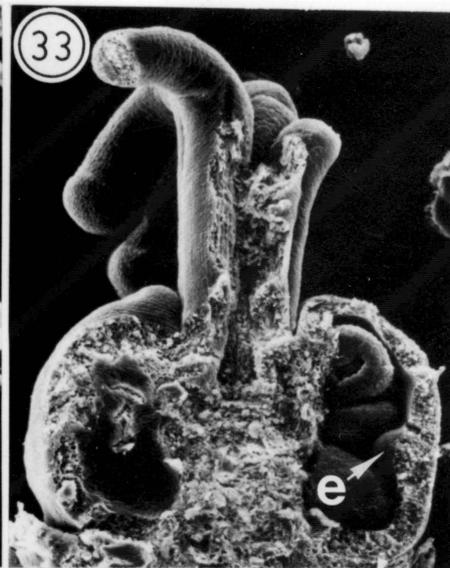
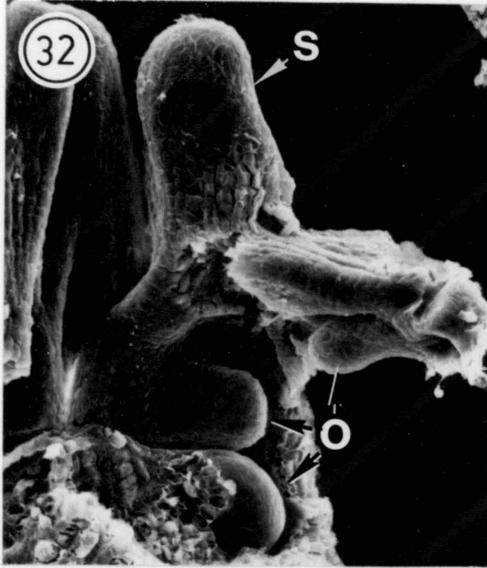


Fig. 38. Longitudinal section of young carpel of Abutilon demissum showing the development of the endoglossum (e) between the middle (o2) and lower (o1) ovules. x265.

Fig. 39-41. Cross sections of portions of the gynoecium of Abutilon demissum at anthesis. x265.

39. Lateral wall showing continuity and development of a multiseriated epidermis (arrows).

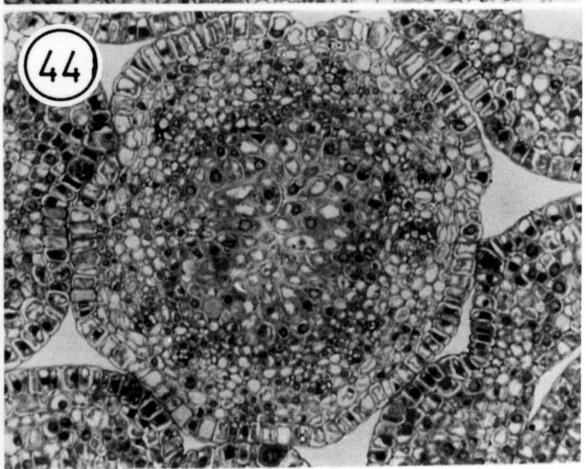
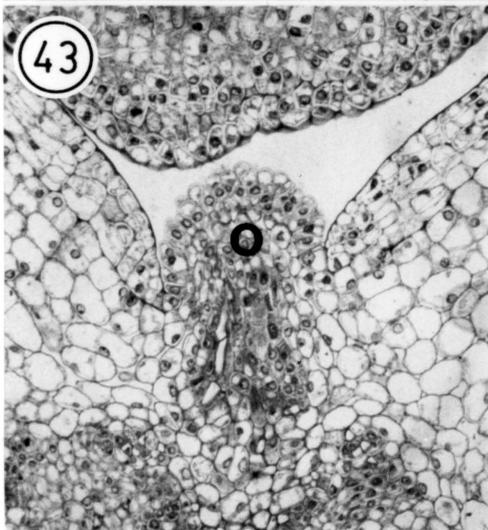
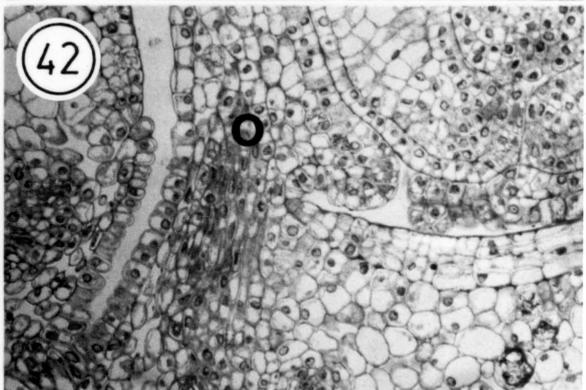
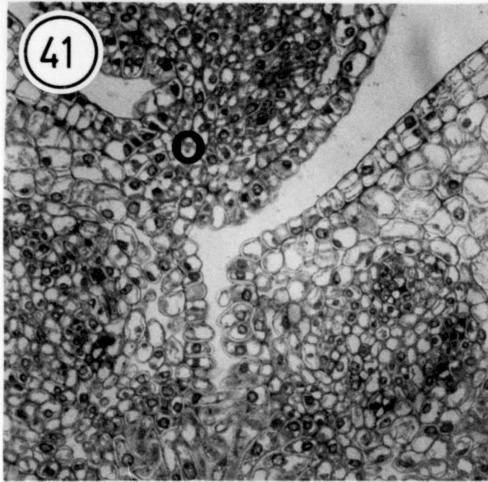
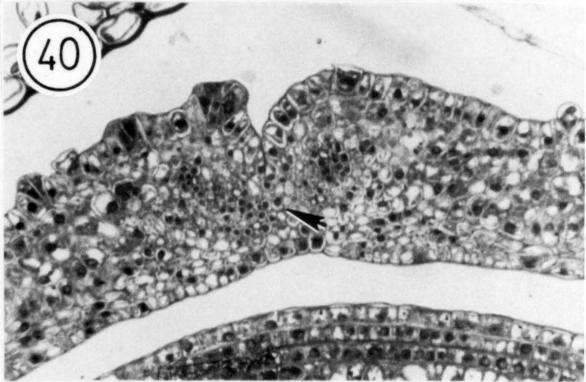
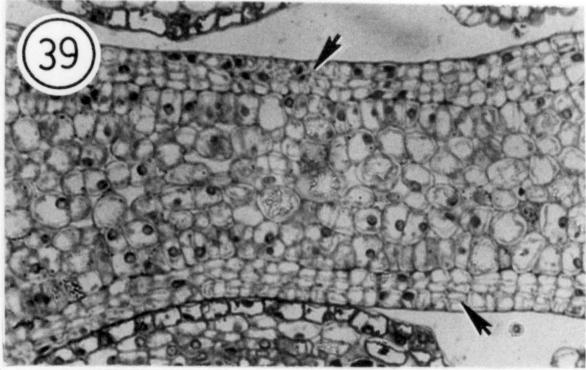
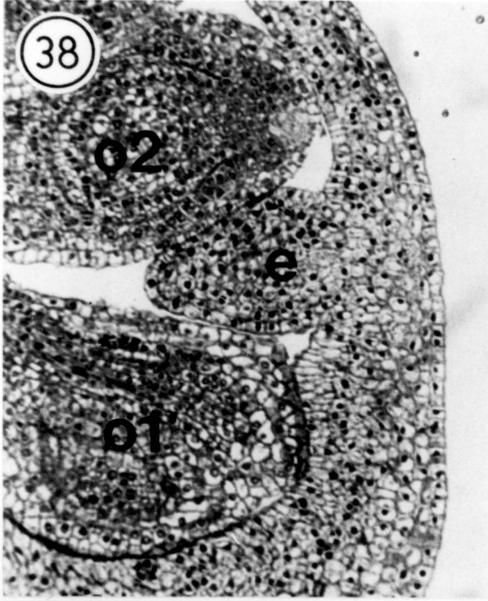
40. Dorsal wall showing locular groove and region of dehiscence (arrow).

41. Lateral insertion (o) of upper ovule.

42. Lateral insertion (o) of middle ovule.

43. Central insertion (o) of bottom ovule.

44. Compound style consisting of 5 styler components.



DEVELOPMENT IN Malacothamnus fasciculatus:

The gynoecium of Malacothamnus fasciculatus originates in an identical manner to that of the two Abutilon species. Here, a continuous ring arises prior to the appearance of any primordia (Fig. 46) and delimits an area comparable to that of Abutilon Theophrasti (Fig. 45a). Ten to fifteen locular depressions develop on its inner flank (Fig. 48) and enlarge through radial expansion (Fig. 45) and zonal growth from below (Fig. 48, 49, 50). By anthesis the gynoecium has produced many stellate trichomes and a prominent bulging of its dorsal walls.

As with the other two species described, the fruit of Malacothamnus fasciculatus shows both a loculicidal and septicidal dehiscence. Sectioned material of the dorsal wall reveals two internal longitudinal thickenings composed of very large, heavily lignified cells (Fig. 53). These thickenings impart a high degree of rigidity to the dorsal wall. Since they flank the region of future loculicidal dehiscence, any external perturbation of the gynoecium would act to effect the separation of the carpel into two halves. Similar to the multiseriated epidermis of the two Abutilon species, the inner thickenings of the dorsal wall are found to be derived from a single surface layer which lines the chamber of the carpel (Fig. 54). In the mature fruit the surfaces of the lateral

walls also become lignified, forming the characteristic pattern of epidermal fibers associated with septicial dehiscence (Fig. 55).

One ovule primordium is initiated per carpel. It originates in a central position directly below the ventral suture (Fig. 49). The "ascending" nature of the ovule is well manifested by the time integumentary layers are present (Fig. 50). At anthesis the ovule fills the cavity of its carpel and maintains a central insertion (Fig. 52).

Malacothamnus fasciculatus is distinguished from the other two species in its time of appearance of style primordia. Here, they initiate and grow well in advance of ovule inception (Fig. 47, 48). The styles elongate as free structures (Fig. 49), secondarily fusing to one another in their lower regions (Fig. 51). Overarching of the style bases does occur to some extent (Fig. 45 d-f) but is less pronounced than that of the two Abutilon species.

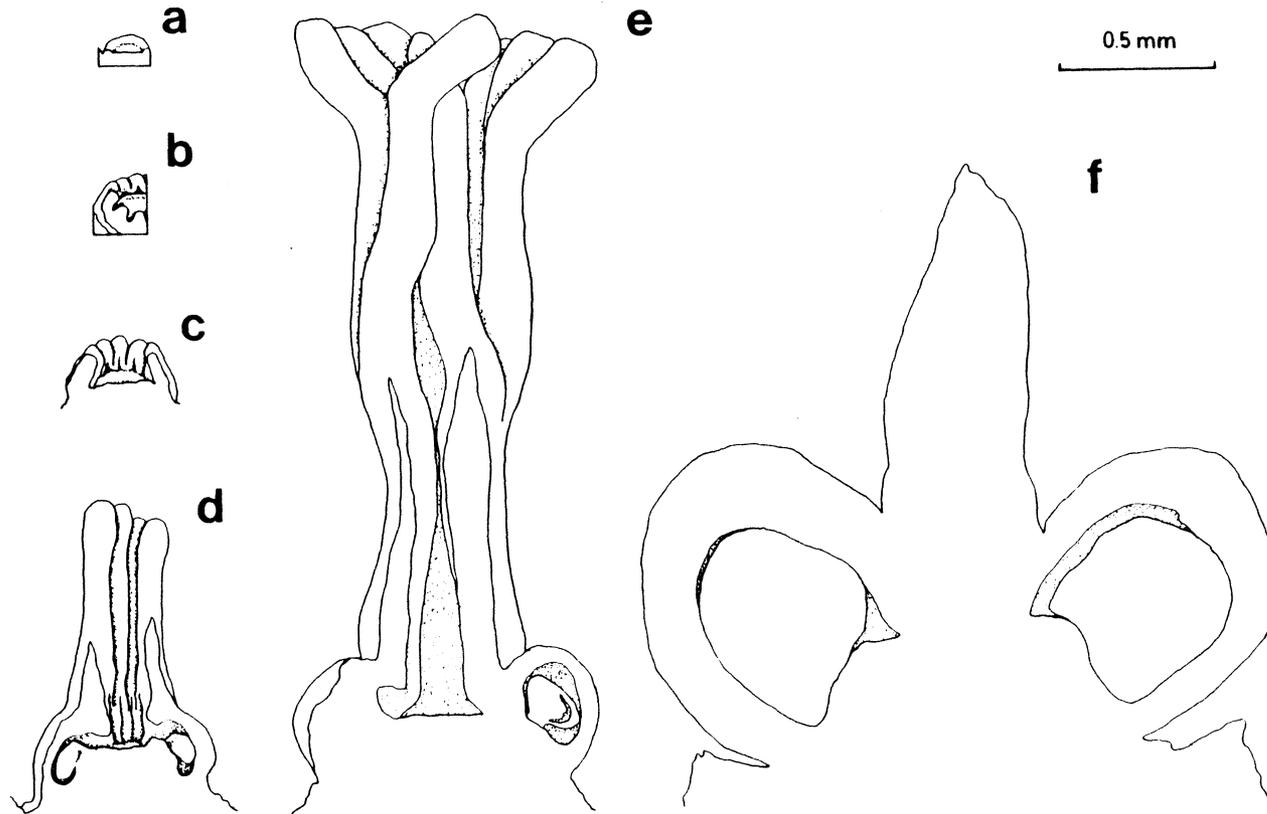


Figure 45. Developmental sequences of Malacothamnus fasciculatus drawn to the same scale.

Fig. 46-51. Scanning electron micrographs of gynoecial development of Malacothamnus fasciculatus.

46. Oblique view showing initiation of gynoecial ring. x540.

47. Cut away side view. Locular depressions (ld) and style primordia (s) have begun to develop. x420.

48. Cut away side view showing free, upward growth of young style (s). x225.

49. Cut away side view. Continued growth of styles. Young ovules (o) are inserted below ventral suture. x75.

50. Close-up of fig. 51 showing central position of ascending ovule (o). x135.

51. Cut away side view. Extensive vertical growth of styles and their fusion to one another. x28.

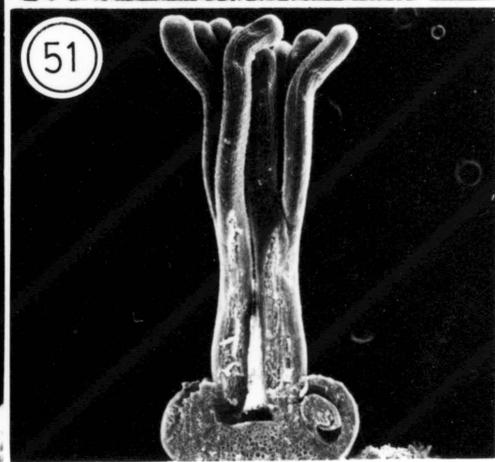
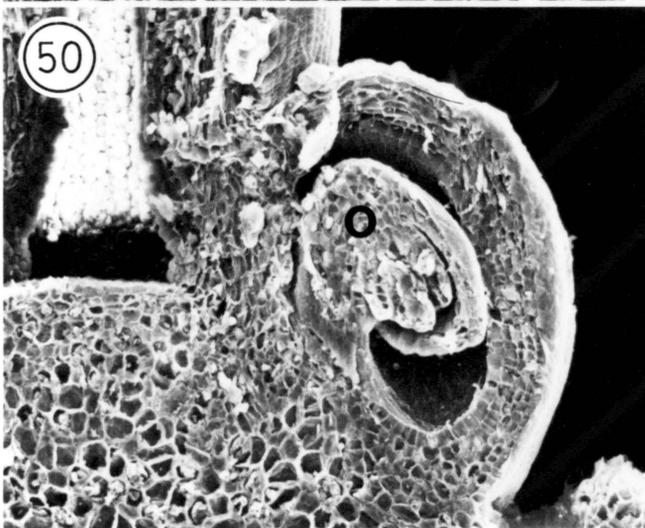
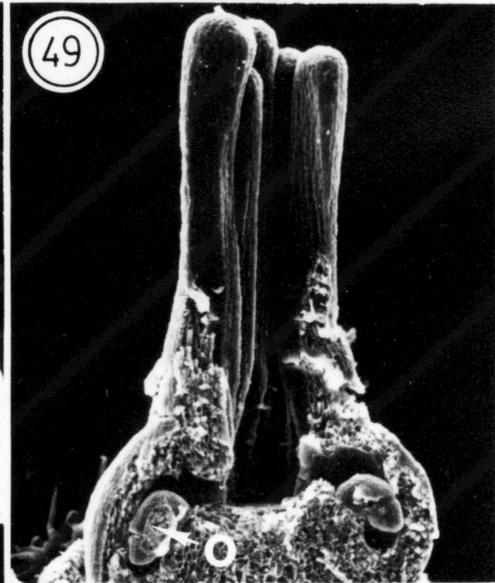
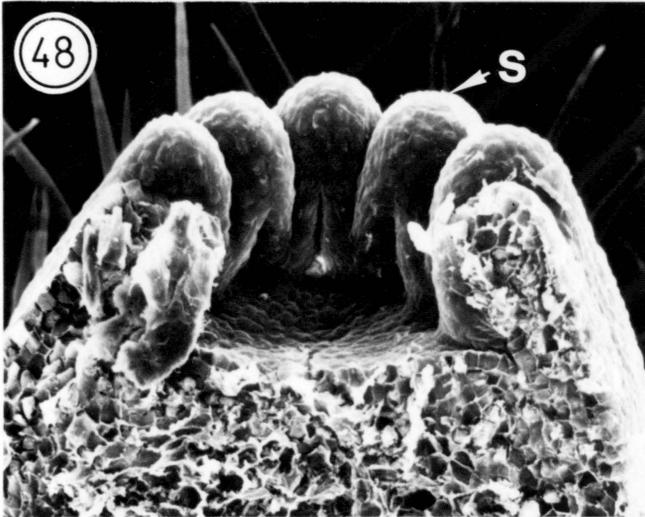
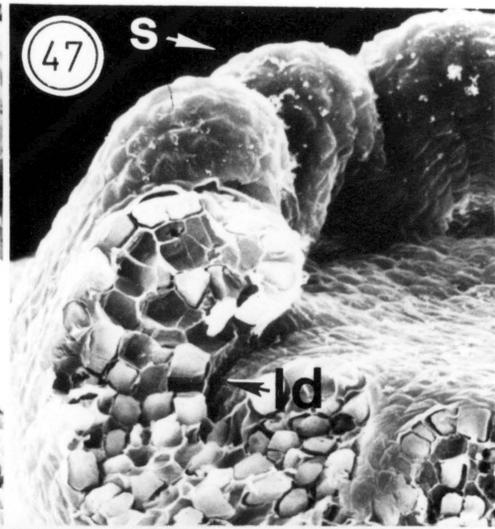
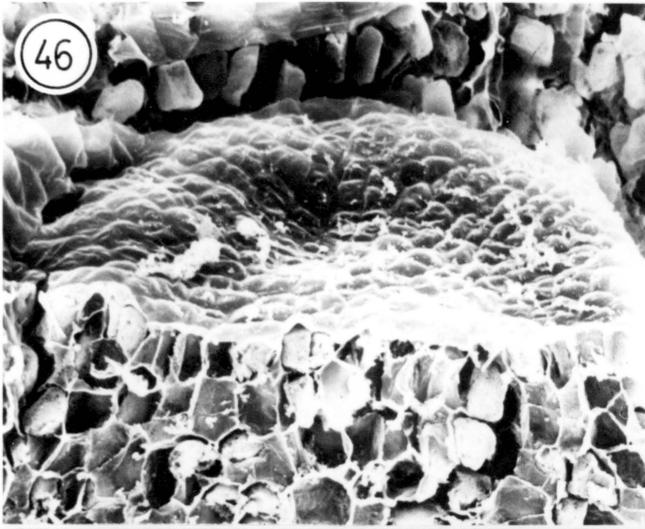


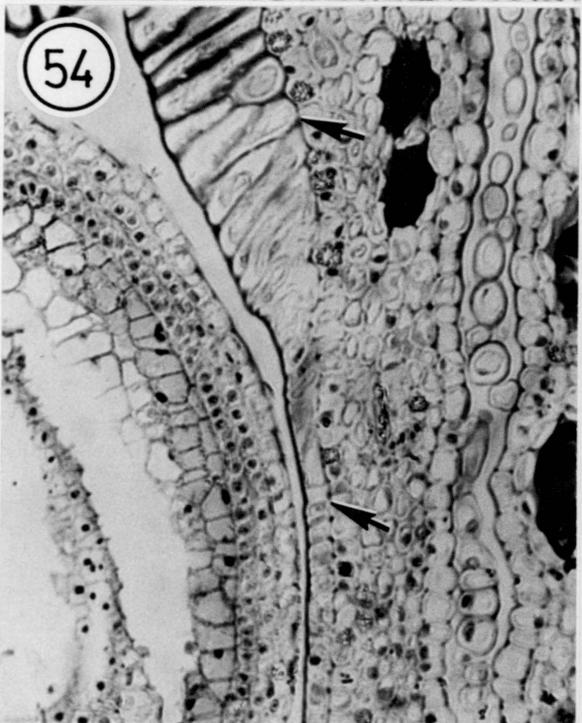
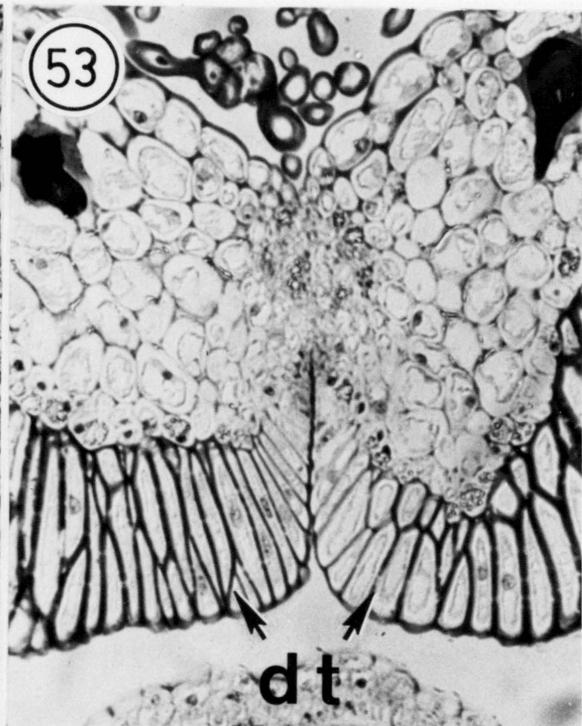
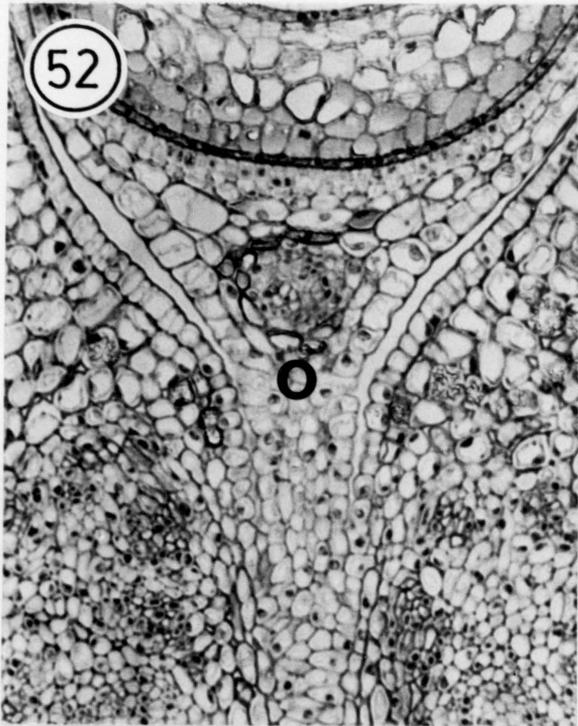
Fig. 52-54. Cross sections of portions of the gynoecium of Malacothamnus fasciculatus. x130.

52. Central attachment of the ovule (o).

53. Portion of dorsal wall showing highly lignified inner dorsal thickening (dt) and region of dehiscence.

54. Origin of the dorsal thickening from the epidermis of the locule (arrows).

Fig. 55. Scanning electron micrograph of the locular epidermis of Malacothamnus fasciculatus showing pattern of lignified fibers. x375.



Chapter V  
DISCUSSION

The original intent of this study had been to provide detailed comparisons of gynoecial development among a group of taxonomically related species of the Malvaceae. The project, however, met with immediate difficulty, as there were problems associated with the interpretation of certain ontogenetic features. In some cases, their resolution had theoretical implications and this necessitated further consideration. Finally, the physical environment in which certain structures develop was found to play an important role in their maturation, and this too was considered to some degree.

Consequently, an array of different conclusions have been made which might be grouped in several different manners. Here, the analysis is presented with respect to the various structures of the gynoecium.

GYNOECIAL RING:

In all three species, the initiation of the gynoecium was marked by the appearance of a continuous, circular bulge or "ring" which preceded the formation of any primordia. This observation, however, is not corroborated by previous

ontogenetic investigations of malvaceous species. Payer (1857) and Sattler (1973) report the appearance of primordia prior to the formation of a bulge for two species of Malva (subtribe Malvinae). Duchartre (1845), however, contradicts this by stating that, with Malva and its relatives, a continuous bulge develops first.

The differences reported here are significant. In Malacothamnus and the two Abutilon species studied, the origin of the gynoecium is very definitely in the form of a continuous ring. What might be inferred by the other descriptions is that different species originate their gynoecia differently. If so, we have before us a potentially important piece of evidence for taxonomic applications.

The discernment of the gynoecial ring in the species studied, however, was quite difficult even when employing electron microscopy at magnifications of 600-1000 times. The works of Duchartre, Payer and Sattler were conducted with light microscopy where resolution, depth of field and magnification are considerably lower. It is possible, then, that these investigators might have had gynoecia in which the styler primordia had been initiated, but were unable to detect the continuous rim underlying them. For this reason, I am unwilling to speculate on the differences presented here,

except to say that future endeavors in this area should give particular attention to this aspect of development.

Van Heel (1978) studied the earliest stages of gynoecial development in members of the tribe Ureneae. He reports the origin of two whorls of carpel primordia, separated in time and alternate with one another. Here, the results are presented in a highly verifiable form and it is concluded that members of the tribe Ureneae initiate their gynoecia in a very different manner than that found in the species considered in this project.

The size of the gynoecial ring that develops was found to differ among the species studied. In Abutilon Theophrasti and Malacothamnus fasciculatus the ring is of comparable diameter, whereas in Abutilon demissum it is considerably smaller (Fig. 2a, 25a, 45a). At the stage where they are first defineable, all three species show carpels of similar dimensions despite the size of the ring on which they develop. This, then, suggests a possible mechanism by which differences in carpel number are achieved - the larger the ring the greater the number of carpels that can be accommodated.

The effect of the physical environment does not end here, as Duchartre (1845) has noted that the androecial tube can

influence the shape of the gynoecial ring (ie. pentagonal tubes produce pentagonal rings). Indeed, it was found in this study that the gynoecial ring originated just inside the androecial tube. Presumably, then, a change in dimensions of the androecium could ultimately result in a difference in the number of carpels that are initiated. The significance of the androecial tube was not taken up in this study, but its consideration in future investigations should provide some important insights.

#### BODY OF THE GYNOECIUM:

The development of the body of the gynoecium, from a ring to a structure complete with locules, lateral walls, etc., was considered at length in the descriptions. Here, all three species develop fundamentally alike. Through processes of overall radial expansion and differential growth, the carpels and their chambers are "molded" from homogeneous tissue with no fusion taking place. Some observations by others, however, are not in accordance with the findings in this study.

Most investigators of gynoecial development in the Malvaceae report that the lateral walls appear and grow inwards across the residual apex, eventually fusing to one another at the center (Duchartre, 1845; van Heel, 1978; Klotz, 1975;

Payer, 1857). Klotz and Payer state that the ventral margins of the carpels fuse to the developing residual apex as well. Klotz further suggests that the carpels fuse laterally to one another in their upper portions. In Abutilon Theophrasti, Abutilon demissum and Malacothamnus fasciculatus, however, none of these fusionary events are found to occur.

Once again, the findings of previous investigators are applied with caution as there exist inherent difficulties with interpretation of development in the body of the gynoecium. Several important factors which might act to influence analysis are considered here.

First, developmental stages must be considered with respect to relative size to one another (eg. Fig. 2, 25, 45). Take, for example, the stage where lateral walls of Abutilon Theophrasti appear and ultimately define the residual apex (Fig. 2b). At this point the residual apex is quite large in comparison to the gynoecium. As development proceeds it dwindles in relative prominence but not in size. Indeed, the residual apex actually enlarges. The lateral walls, therefore, "grow" outward rather than towards the interior. Likewise, the ventral sutures do not fuse to restrict the opening. The small ventral slits of figure 2h are ultimately attributable to the margins of the locular depressions (Fig. 2b-g). Through development, their

circumference does not decrease but, if anything, becomes more pronounced.

Finally, developmental processes such as those found in the gynoecia of the Malvaceae tend to run counter to expectations construed from the "classical" theory of carpel origin. Here, a very singular structure (the gynoecial ring) gives rise to a body of distinct, repeating units. Likewise, the gynoecia studied show complete continuity of carpels with the proximal region of the residual apex, making delimitation of the two structures impossible. Such peculiarities have led Klotz (1975) to draw dotted (imaginary) lines in order to distinguish carpels from the apex. This, in itself, might not present difficulties except that he then goes on to describe the "postgenital fusion" that occurs.

As noted previously, Bakeridesia is closely allied with Abutilon. Klotz's diagrams, likewise, reflect similarities in gynoecial morphology that strongly suggest an identical pattern of development about the residual apex. Despite his recognition of the "congenital" growth of carpels and residual apex during early stages of development, it appears that Klotz secondarily applied a model more congruous with traditional concepts when considering mature gynoecia. Is the "postgenital" fusion reported by him actual or inferred? This

is a necessary question to ask, for if, indeed, such a process does occur, then we have here an example of a closely related taxon which differs significantly in its development from those considered in this work.

Difficulties aside, development of the body of the gynoecium in the Malvaceae does have a common denominator since most investigators will agree that at least some zonal growth occurs. Aspects of the work of Duchartre (1845) and Payer (1857) represent the only attempts at consideration of gynoecial development in the tribe Hibisceae. Here, both report that radial septa move towards the interior of the gynoecium and "meet". A cursory look at the fruits of some members from this group suggests that, indeed, such a mechanism of development may exist. In keeping with the distinctively different pattern of inception of the gynoecia in the Ureneae, van Heel (1978) reports that the second whorl of carpels abort cavity and locule formation and grow only styles.

It appears, then, that significant differences in gynoecial ontogeny do exist among several of the tribes of the Malvaceae. In the final analysis, however, a number of gynoecia should be reconsidered in light of the evidence presented in this study, particularly as regards the tribe Malveae.

## DEHISCENCE:

All three species studied are known to exhibit both a loculicidal and septicidal dehiscence. Both of these processes were found to be effected by differentially strengthened tissues.

In the case of loculicidal dehiscence, separation was restricted to a narrow region between two dorsal vascular bundles. Malacothamnus fasciculatus differed from the two Abutilon species in having two, internal, longitudinal thickenings flanking the future site of dehiscence. Whereas fruits of Abutilon theophrasti split along their dorsal walls upon drying, a different strategy is proposed for Malacothamnus. The inner reinforcements of the latter impart a high degree of rigity to the dorsal wall such that any forces would be transmitted towards effecting dehiscence. This feature, therefore, suggests that dehiscence may be prompted by external perturbations.

At first glance the dorsal thickenings of Malacothamnus suggest a significantly different fruit morphology to that of the two Abutilon species. Closer examination, however, reveals that they are derived from a single surface layer that lines the interior of the carpel. This same epidermal layer

was shown to have a propensity for lignification and cell division along the lateral walls of Abutilon Theophrasti and Abutilon demissum. Although functionally important and striking in appearance, the dorsal thickenings are, therefore, found to be homologous with the multiseriate epidermis of the other two species considered.

The multiseriate epidermis is, itself, a rather unique feature of rare occurrence among vascular plants (Eames and McDaniels, 1947). Where found, this tissue is generally attributed some special function (e.g., storage, water retention, etc.). Among the two Abutilon species studied, the multiseriate epidermis is restricted solely to the inner surfaces of the carpels. The distinctness and highly localized nature of this tissue is, therefore, presumed to play an important developmental role in the septicidal dehiscence that later occurs.

The disarticulation of carpels from one another was a disconcerting feature to find among the species studied. All three were known to produce common lateral walls through zonal growth, yet, during late maturity of the gynoecium, adjacent carpels would "pop" apart from one another as if hardly attached. The behavior of the fruits might have suggested that the carpels were indeed fused to one another along their

lateral walls. The septicidal dehiscence, then, would have implied a simple "loosening" along the fused surfaces, a condition reported to be the norm by Eames and McDaniels (1947) and Addicott (1982).

As outlined in the descriptions, the lateral walls of all three species studied were found to develop three layers of differentially strengthened tissues. The two outer layers of multiseriate epidermis differentiate into heavily lignified fibers, whereas the inner layer remains as predominantly thin-walled parenchyma. Separation, then, was found to occur randomly along the weaker, internal tissue, causing uneven surfaces to be produced (Fig. 24).

We see then that, although not outwardly apparent, the actual mechanism of septicidal dehiscence tends to support the observation that lateral walls are a product of zonal growth. Separation does not occur along an inherent, predetermined surface (such as former fusion margins) but, rather, through a secondarily derived zone of differentially weaker tissue.

Identical modes of loculicidal dehiscence were reported by Hochreutiner (1920) for a number of other members of the subtribe *Abutilinae*. Klotz (1975) notes a similar pattern for *Bakeridesia*. Additionally, his description of the histology

of the lateral wall is identical to that found in the species studied.

Finally, as carpels disarticulate from one another, they leave behind a structure known as the "columella". Close examination of the dehisced fruit of Abutilon Theophrasti has revealed that the columella is a compound structure consisting of residual apex, parts of lateral walls and remnant funiculi (Fig. 22). Its enigmatic nature is better understood in light of the ontogenetic evidence.

The zonal growth discussed at length earlier manifests itself not only in the region surrounding the locules but throughout the "core" as well. The residual apex, then, does not grow upward to keep pace with the developing carpels but is uplifted with them (Fig. 7, 8). Evidence is supplied not only by the longitudinal files of cells (indicative of a rib meristem) that are produced in this region, but also by the relative position of ovules which, here, retain a constant relative position with the carpel/residual apex juncture throughout development (Fig. 6, 7, 8). We find, then, that there are no zones of inherent weakness resulting from the fusion of two surfaces, since no such process has occurred. Consequently, the notion that "carpels" separate from a "receptacle" is not truly applicable here.

## OVULES:

The pattern of ovule initiation and development was found to be fundamentally identical between Abutilon Theophrasti and Abutilon demissum. That the single ovule of Malacothamnus fasciculatus is homologous with the bottommost ovule of the Abutilon species is borne out by its central insertion directly beneath the ventral suture.

The acropetal initiation of ovule primordia in the two Abutilon species supports the contention by Bates (1968) that the uniovulate condition is derived from pluriovulate carpels. Here, a possible mechanism is suggested, as abbreviation of ovule number would tend to proceed in a basipetal direction, beginning with the last developed (or yet to appear) ovules first. One would expect, then, that the uniovulate condition would reflect the abortion of all upper ovules, with the remaining one being centrally inserted below the ventral suture. This indeed appears to be the case with Malacothamnus fasciculatus.

A cursory look at several members of the subtribe Malvinae (a taxon characterized by uniovulate carpels) also reveals a central position of the single ovule beneath the ventral suture, implying that these too have a similar relation with

pluriovulate species. Nothing is known, however, of the single, pendulous ovule of the Sidinae. How does its development compare with the ascending ovules of the Malvinae? Finally, how similar is ovule initiation in the many-seeded gynoecia of the tribe Hibisceae? An extensive survey of the spatial and temporal patterns of ovule initiation in the Malvaceae would appear to be an endeavor of important taxonomic consequence.

#### STYLES:

In all three species considered, inception of style primordia began in an apical position on the gynoecial ring. Later development of these primordia was found to contribute little if any to subsequent growth of the body of the gynoecium. Of the various investigations into gynoecial development of the Malvaceae, only Duchartre (1845) makes a direct reference to this ontogenetic phenomenon.

Subsequent style development was marked by the elongation of style primordia as free structures. These, then, became secondarily united to one another in their lower regions, thereby representing the first and only true fusionary event observed in this study.

In Malacothamnus fasciculatus, one important difference in style development was observed. Here, style primordia are found to originate in advance of the initiation of ovules. In fact, the style primordia are already quite elongated by the time locule formation has begun (Fig. 48). Herein lies the possibility of an additional mechanism for determining ovule number.

The precocious development of style primordia appears to foreshorten the upward growth of the gynoecia ring. This, in turn, could potentially restrict the extent of cavity formation and, ultimately, the number of ovules that might originate there. Although this is speculative, the ramifications are highly significant. The question arises as to what pattern of style initiation is to be found in the uniovulate taxa of other Malvaceae. Or, what might be the condition in the many-seeded Hibisceae? No previous investigations have addressed this aspect of gynoecial development. Its potential importance, therefore, remains unknown.

#### ENDOGLOSSUM:

The nature of the endoglossum was considered rather extensively by Hochreutiner (1920). As noted earlier, it is

generally represented as an internal appendage which divides the cavity of the carpel. A number of divergent forms, however, are reported throughout the Malvaceae.

The presence of an endoglossum was known to exist in Abutilon demissum (Fryxell, 1980) and particular attention was therefore given to it with respect to its development. Here, it was found to be derived from a simple ingrowth of the dorsal wall, with complete continuity of epidermal and ground tissues to the latter. No distinctive tissue formation could be associated with the endoglossum and neither of the other two species considered provided any hint as to its origin. The inner dorsal thickenings of Malacothamnus fasciculatus obviously had no relation with it.

Bates (1968) and Fryxell (1980) consider the endoglossum to be of polyphyletic origin. In the case of Abutilon demissum, the structure is not a complex one and might be easily derived. One is still left with the perplexing questions, however, as to how and why endoglossa are found to recur in various unrelated taxa of the Malvaceae.

## Chapter VI

### SUMMARY

The gynoecia of all three species considered in this study originate not as individual carpel primordia but rather as a continuous ring. Processes of continued radial expansion and differential zonal growth give rise to the mature body of the gynoecium with no observable fusion taking place. Later manifestations of distinctness and separation of carpels represent secondarily acquired traits. Consequently, the mature gynoecia of the Malvaceae cannot be reliably used to infer early developmental events.

The physical environment in which carpels originate is proposed to play a role in determining carpel number. Carpel size at inception does not vary considerably among the different species surveyed here. Ring size, however, does and this presumably dictates carpel number by the upward limit of what its circumference can ultimately accommodate.

The uniovulate condition appears to be derived from the pluriovulate one through several interrelated developmental events. On the basis of acropetal initiation of ovules in Abutilon species and the precocious development of style primordia in Malacothamnus fasciculatus, a mechanism for the

origin of the uniovulate carpel is proposed. Here, early style growth may limit zonal growth of the gynoecial base so that the acropetal series of ovule initiations is disrupted, leaving only a single basal one.

The study of gynoecial development in this group has been hindered by certain problems of interpretation (e.g., Duchartre, 1845; Klotz, 1975; present account). These include difficulties in conceptualization of developmental processes and their reconciliation with preconceived views of the evolutionary origin of gynoecia. Consideration of relative size among successive stages is crucial, since the affect of radial growth is otherwise easily overlooked.

Despite the differences of their mature gynoecia, the three species studied were determined to be strikingly similar in development, thereby supporting the close affinities attributed to them. In the final analysis, however, conclusive statements regarding the systematic implications of the ontogenetic patterns observed would be premature. Too few taxa have been studied and those that have should be reassessed in light of the developmental phenomena presented here.

## LITERATURE CITED

- Addicott, F. T. 1982. Abscission. Univ. of Calif. Press. Berkley. 369 p.
- Barabe, D. et J. Vieth. 1979. Le concept de fusion en morphologie vegetale chez Payer et chez Van Tieghem. Acta Biotheoretica. 28, 3: 204-216.
- Bates, D. M. 1968. Generic relationships in the Malvaceae, Tribe Malveae. Gentes Herb. 10: 117-135.
- Bentham, G. 1862. Malvaceae, pp. 195-213, *In*: G. Bentham and J. D. Hooker, Genera Plantarum. Vol. I, 1040 p. London.
- Berlyn, G. P. and J. P. Miksche. 1976. Botanical microtechnique and cytochemistry. Iowa State Univ. Press. Ames, Iowa. 326 p.
- Cusick, F. 1966. On phylogenetic and ontogenetic fusions, pp. 170-183, *In*: E. G. Cutter, ed. Trends in plant morphogenesis. Wiley and Sons, Inc. N.Y. 329 p.
- De Candolle, A. P. 1819. Theorie elementaire de la botanique ou exposition des principes de la classification naturelle. 2nd ed. Paris.
- Duchartre, M. P. 1845. Observations sur l'organogenie de la fleur dans les plantes de la famille des Malvacees. Ann. Sci. Nat., Serie 3., 4: 123-150.
- Eames, A. J. 1961. Morphology of the angiosperms. McGraw-Hill Book Co. New York. 518 p.
- \_\_\_\_\_ and L. H. McDaniels. 1947. An introduction to plant anatomy. 2nd ed. McGraw-Hill Book Co. New York. 767 p.
- Edlin, H. L. 1935. A critical revision of certain taxonomic groups of the Malvales. New Phytol. 34: 1-20, 122-143.
- Esau, K. 1965. Plant anatomy. John Wiley and Sons. New York.
- Fryxell, J. E. 1983. A revision of Abutilon sect. Oligocarpae (Malvaceae), including a new species from Mexico. Madrono. 30(2): 84-92.
- Fryxell, P. A. 1968. A redefinition of the tribe Gossypieae. Bot. Gaz. 129: 296-308.

- \_\_\_\_\_. 1975. Generic relationships of Decaschistia (Malvaceae) and the description of a new tribe, Decaschisteeae. *Amer. J. Bot.* 62(2): 172-175.
- \_\_\_\_\_. 1980. Malvaceous miscellany, including new species from Mexico and Brazil. *Brittonia* 32(2): 262-268.
- Goethe, J. W. von. 1790. Versuch die metamorphose der pflanzen zu erklaren. Gotha.
- Gould, S. J. 1978. Ontogeny and phylogeny. Harvard Univ. Press. Cambridge, Mass. 501 p.
- Heel, W. A. van. 1978. Morphology of the pistil in Malvaceae - Ureneeae. *Blumea* 24(1): 123-137.
- Hochreutiner, B. P. G. 1920. Organes carpigues nouveaux ou meconnus chez les Malvacees. *Ann. Conserv. Jard. Bot. Geneve.* 21: 347-387.
- Johansen, D. A. 1940. Plant microtechnique. McGraw-Hill Book Co. New York. 523 p.
- Kearney, T. H. 1951. The American genera of Malvaceae. *Am. Midl. Nat.* 46: 93-131.
- Klotz, L. H. 1975. Anatomy of the gynoecium in two species of Bakeridesia (Malvaceae). *Amer. J. Bot.* 62(10): 1053-1059.
- Leinfellner, W. 1950. Der Bauplan des syncarpen Gynozeums. *Osterr. bot. z.* 97: 403-436.
- Lorch, J. 1963. The carpel - a case history of an idea and a term. *Centaurus* 8: 269-291.
- Meeuse, A. D. J. 1965. Angiosperms past and present, Vol. 11, In: L. Chandra, ed. Advancing frontiers of plant science. Insitute for the advancement of sciences and culture. New Delhi. 228 p.
- Melville, R. 1962. A new theory of the angiosperm flower: I. The gynoecium. *Kew Bull.* 16: 1-50.
- Payer, J. B. 1857. Traite d'organogenie comparee de la fleur. Librairie de Victor Mason. Paris.
- Rao, V. S. 1968. Necessity for a re-evaluation of the theories concerning the origin of the inferior ovary. *J. Biol. Sci.* 11: 61-62.

- Ross, R. 1982. Initiation of stamens, carpels, and receptacle in the Cactaceae. *Amer. J. Bot.* 69(3): 369-379.
- Sattler, R. 1965. Perianth development of Potamogeton richardsonii. *Amer. J. Bot.* 52(1): 35-41.
- \_\_\_\_\_. 1973. Organogenesis of flowers. A photographic text-atlas. University of Toronto Press. Canada. 207 p.
- \_\_\_\_\_. 1974. A new approach to gynoecial morphology. *Phytomorphology*. 24: 22-34.
- \_\_\_\_\_. 1978. 'Fusion' and 'continuity' in floral morphology. *Notes Roy. Bot. Gard. Edinb.* 36: 397-405.
- Saunders, E. R. 1930. The evolution of the syncarpous gynoecium. *Proc. 5th Int. Bot. Congr. Sect. M.* pp. 183-184. Cambridge.
- \_\_\_\_\_. 1936. On certain features of floral construction and arrangement in the Malvaceae. *Ann. Bot.* 50: 247-282.
- Schumann, K. 1895. Malvaceae, pp. 30-53, *In*: A. Engler and K. Prantl, *Nat. Pflanzenfam.* III(6), 254 p. Leipzig.
- Singh, V. 1979. Early floral development in Digitalis purpurea. *Phytomorphology*. 29: 239-245.
- Takhtajan, A. 1972. Patterns of ontogenetic alterations in the evolution of higher plants. *Phytomorphology*. 22: 164-170.
- Thompson, J. M. 1935. The apocarpous nature of modern flowering. *Proc. 6th Int. Bot. Congr.* 2: 122-141. Amsterdam.
- Troll, W. 1939. Die morphologische natur der karpelle. *Chron. Bot.* 5: 38-41.
- Wardlaw, C. W. 1968. Morphogenesis in plants: A contemporary study. Methuen and Co. London. 451 p.
- Wilson, C. L. 1942. The telome theory and the origin of the stamen. *Amer. J. Bot.* 29: 759-764.

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COMPARATIVE ANALYSIS OF OVARY DEVELOPMENT  
IN SELECTED MEMBERS OF THE SUBTRIBE ABUTILINAE (MALVACEAE)

by

Garrie Davis Rouse

(ABSTRACT)

Abutilon Theophrasti, Abutilon demissum and Malacothamnus fasciculatus were each studied with respect to their gynoecial development. Data from these taxa was considered in a comparative manner in order to 1) discern the possible homology of certain ovarian structures and 2) evaluate the use of gynoecial characters in Malvaceae systematics. All three species studied were found to strikingly similar in the initiation and early ontogeny of their gynoecia despite differences in the mature fruits. Development of the body of the gynoecium showed no evidence of fusionary processes taking place. Despite marked distinctness among neighboring carpels in mature fruits, dorsal bulging and regions of dehiscence are found to be secondarily acquired traits which cannot be used to infer early developmental events. Possible evolutionary mechanisms are proposed which explain the differences in carpel and ovule number found among these three taxa.