2000

Floral Ontogeny and Phylogeny in Malvaceae.

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FLORAL ONTOGENY AND PHYLOGENY  
IN MALVACEAE  
VOLUME I

A Dissertation  
Submitted to the Graduate Faculty of the  
Louisiana State University and  
Graduate College  
in partial fulfillment of the  
requirements for the degree of  
Doctor of Philosophy  
in  
The Department of Biological Sciences

by

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December 2000
ACKNOWLEDGMENTS

This author wishes to express her appreciation to all members of her advisory committee. I am particularly grateful to Dr. Shirley C. Tucker, Committee Chair, for her guidance, patience, and support. Her knowledge of floral development and editing skills greatly enhanced this project. Having the opportunity to work with her has truly been a privilege and her friendship is something I will always treasure. Dr. Paul Fryxell's input as an expert on the plant family Malvaceae has been of great value. My thanks also go to Dr. Thomas Wendt, Marie Standifer, Dr. Lowell Urbatsch, Dr. Andrew Douglas, Dr. Katherine Kantz, and to the many others who assisted with various aspects of this research. I also wish to acknowledge the understanding and encouragement provided by my family and friends during this long process.

Plant material was obtained with the cooperation of Fairchild Botanical Gardens and Montgomery Foundation in Florida, Missouri Botanical Gardens, the USDA seed bank in Iowa, Dr. Phil Evans (horticultural plot at Louisiana State University), Dr. Paul Fryxell (collection in greenhouse at Texas A & M University), Dr. John La Duke (collection at University of North Dakota), and several private land owners. Peggy Reed at Louisiana State University Burden Plantation provided greenhouse space and a garden plot and assisted with watering.

Technical advice was provided by Sharon Mathews in the electron microscopy facility for the Basic Sciences at Louisiana State University. The Biology Department at East Carolina University (in Greenville, North Carolina) graciously allowed access to their darkroom facilities for preparation of final photographic plates and Beaufort County Community
College (in Washington, North Carolina) made available light microscopes in the teaching labs.

Funding for this project came from Dr. Tucker's Boyd Professor account. Additional resources were provided by the National Science Foundation, grant number NSF92-07671.
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ABSTRACT

Floral ontogeny in representatives of Malvaceae was compared using scanning electron microscopy. Many aspects of floral development have been resolved by this research, including the presence of a petal-stamen ring meristem in malvaceous taxa. There are several ontogenetic pathways to the formation of this ring meristem; in addition, common petal-stamen mounds are usually present during some stage of development. Stamen proliferation is achieved by partitioning of the ring meristem and furcation of common stamen primordia. Time of initiation overlaps between the corolla and the androecium, and between the androecium and the gynoecium. Helical initiation occurs in the outer organ whorl or whorls and simultaneous initiation occurs in the inner organ whorls or the sets of organs composing these whorls. Ring meristems are sometimes present in bractlet, sepal, and carpel whorls. This research details the complex development leading to the multistaminate androecial columns and the development of the syncarpous gynoecia. Several unusual features are elucidated such as common bractlet primordia, displacement of bractlets, and suppression of organs. Features that distinguish bractlets from floral bracts and from sepals are discussed. The idea that bifurcation and partitioning events are the likely causes of the bisporangiate condition is refuted. Although the exact mechanism behind the formation of sterile teeth was not ascertained, several factors are identified as sometimes contributing, and some are ruled out as causal. In addition, examination of selected taxa in the sister families Bombacaceae and Sterculiaceae reveals the development of other floral structures such as androgynophores, more than one stamen whorl in the androecium,
apocarpous gynoecia, and multistamen meristematic pads. The ontogenetic data has been used to characterize the tribes and distinguish among certain genera in Malvaceae as well as to delineate the family. A cladistic analysis utilizing ontogenetic floral data and morphological data shows that Malvavisceae, Gossypieae, and Malveae are monophyletic, but Hibisceae is paraphyletic. Several evolutionary trends in character traits are revealed and some clarification is provided about phylogenetic relationships within the Malvaceae.
BACKGROUND INFORMATION ON MALVACEAE

Malvaceae is a large, widespread and economically important plant family. Despite the large diversity of morphological forms, little research has focused on floral development in the family. Ontogenetic studies are needed to answer many morphological questions about development in the rather specialized flowers of members of Malvaceae. In addition, many genera are in questionable position within a tribe or even within the family. More studies are needed to clarify the taxonomy and phylogeny within the family; and floral ontogeny is a promising source of new information.

This chapter gives some background information about the family, summarizes relevant research that has been done, and outlines the goals of this research.

**General description**  -- Members of the Malvaceae family are characterized as herbs, shrubs, or trees principally from tropical and subtropical regions, but with a few genera from temperate regions. The roots are fibrous or woody, and sometimes fleshy in perennial herbs. The stems may be erect, procumbent, or repent. The leaves are alternate and stipulate (the stipules rarely suppressed) with hairs that are stellate, simple, prickly, glandular or rarely lepidote. Leaf shape can be ovate or lanceolate and entire, variously lobed, dissected, or toothed (Hutchinson, 1967; Christensen, 1986; Cronquist, 1988; Fryxell, 1988).

Floral symmetry is generally actinomorphic (with regard to the perianth) and flowers are bisexual or rarely unisexual. Only a few species
are dioecious. The flowers are solitary or fasciculate in the axils of the leaves or grouped in inflorescences (usually racemes or panicles, sometimes spikes or scorpionid cymes, rarely umbels or heads). An involucel may be present or absent. The calyx is synsepalous and may be truncate, five-toothed, five-lobed, or five-parted. The corolla consists of five distinct petals that are usually clawed and are adnate to the base of the staminal column. The androecium is monadelphous, consisting of numerous (rarely reduced to five) stamens. The anthers are reniform and unilocular (bisporangiate). The flowers have a superior gynoecium of 3-40 carpels and 1-40 styles. Stigmas may be truncate, capitate, or decurrent. Fruit type is a schizocarp or capsule, sometimes a berry. Seeds are reniform or turbinate and may be pubescent or glabrous. Rarely the seeds of some taxa are arillate (e.g. Hampea). Base chromosome numbers are \( x = 5, 6, 7, 8, 9, 10, 11, 13, 14, 16, 17, 18, 19, 20, 21, 25, \) and \( 28 \) (Hutchinson, 1967; Christensen, 1986; Cronquist, 1988; Fryxell, 1988).

**Distribution and center of origin** -- Malvaceae is principally American, although it is well represented in the Old World as well, with diversification in Australia, the Mediterranean, the Middle East, Africa, and Madagascar. Its center of origin is probably in South America, with an additional region of diversification in Mexico that is separate from its South American center. Mexico has a richer mallow flora than adjacent areas of Central America, and it contains a large number of endemic genera and species (Fryxell, 1988). Current estimates place the number of genera in Malvaceae at well over a hundred (Table 1.1).

**Economic importance** -- Malvaceae has many economically important members. *Gossypium*, from which cultivated cotton is derived, has
<table>
<thead>
<tr>
<th>Gossypieae¹</th>
<th>Hibisceae²</th>
<th>Malvavisceae³</th>
<th>Malveae⁴</th>
<th>Decaschisteae⁵</th>
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<tr>
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<td>Gourmania</td>
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<td>Bastardioptis</td>
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<td>Helicteropsis</td>
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<td>Hibiscadelphus</td>
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<td>Hymenocalyx</td>
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<td>Corynabutilon</td>
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<td>Julostylis</td>
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<td>Ketnia</td>
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<td>Kydia d</td>
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<td>Hochreutinera</td>
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<td>Muenchhusia</td>
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<td>Hoheria</td>
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<td>Neohumbertiella</td>
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<td>Horsfordia</td>
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<td>Papuodendron</td>
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<td>Iliamna</td>
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<td>Pariti</td>
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<td>Kearnemalvastrum</td>
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<td>Peltoestegia</td>
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<td>Kitaibelia</td>
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<td>Pentagonocarpus</td>
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<td>Krapovickasia</td>
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<td>Pentasperma</td>
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(Table continued)
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<tr>
<th>Gossypieae¹</th>
<th>Hibisceae²</th>
<th>Malvaviscææ³</th>
<th>Malveae⁴</th>
<th>Decaschistææ⁵</th>
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<tr>
<td><strong>Pseudopavonia</strong></td>
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<td><strong>Radyera</strong></td>
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<td><strong>Trionum</strong></td>
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<td>Pseudoabutilion</td>
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<td>Rhynchosida</td>
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<td>Tetrasida</td>
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<td>Urocarpidium</td>
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<td>Wissadula</td>
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Note: Where conflicts in placement occur, the more recent taxonomic treatment has been used except for ². Priority was given to information obtained from Fryxell. More recent estimates, which probably take into account expected taxonomic revisions, place approximately 110 genera in the Malvaceae (La Duke and Doebley, 1995; Fryxell, personal communication).  

¹ Includes Montezuma and Thespesiopsis.  
² Placed in Malveae by Bates (1968) and Bates and Blanchard (1970).  
³ Includes Blanchetiastrum, Codonochlamys, Goethea, Lopimia, and Triplochlamys.  
⁴ In some treatments it is referred to the Bombacaceae.  

⁵ Fryxell, 1975.
had an enormous impact on the economy and history of mankind (Fryxell, 1988). In addition to the fibers (actually epidermal trichomes) being used in materials, the seeds are a source of cotton-seed oil (Hutchinson, 1967). Many genera are cultivated for ornamentals; among the better known are *Abutilon*, *Alcea*, *Althaea*, *Hibiscus*, and *Malva* (Heywood, 1985; Fryxell, 1988). Other mallows are used as food (including *Abelmoschus esculentus* or okra); as a condiment (*Hibiscus sabdariffa*); as forage (*Malva parviflora*); as bast fibers for cordage, sacks, and paper (some species of *Abutilon*, *Sida*, *Hibiscus*, *Hampea*, and *Robinsonella*); and as a minor source of wood for construction, furniture, and other uses. Malvaceae also includes a significant number of weeds such as *Sida*, *Malva*, *Malvastrum*, and *Anoda* (Fryxell, 1988).

**Taxonomy and phylogeny of the order** — Malvaceae is in the order Malvales, which traditionally includes the Bombacaceae, Elaeocarpaceae, Sterculiaceae, and Tiliaceae. Elaeocarpaceae, which is believed to be the most archaic, stands somewhat apart from the rest of the order, but is still sufficiently closely related that it has often been included in the Tiliaceae. Malvaceae, Sterculiaceae, Bombacaceae, and Tiliaceae (often referred to as the core families) are closely allied; and there has often been controversy about their interfamilial limits. Early taxonomic treatments of the order were described by Baillon (1875), Maout and Decaisne (1876), Edlin (1935), Benson (1957), and Engler (1964). Some taxonomic treatments place Sarcoleaenaceae and Sphaerosepalaceae in the Malvales, but Cronquist (1988) concluded that they are better referred to the Theales. Recently, it has been proposed that Malvaceae be expanded to comprise all core Malvales and subdivided into various subfamilies (Judd and Manchester, 1997; APG, 1998; Baum, Alverson, and Nyffeler, 1998; Bayer et al., 1999) and that the
Malvales be revised to include the core families and an assortment of additional families (Dahlgren, 1980; Thorne, 1992; APG, 1998; Baum, Alverson, and Nyffeler, 1998; Alverson et al., 1998, 1999: Bayer et al., 1999).

In a broad cladistic analysis using chloroplast \textit{rbcL} sequences, Chase et al. (1993) placed the Bombacaceae (represented by \textit{Bombax}) as most primitive or basal of the core families, followed by Tiliaceae (\textit{Tilia}). Sterculiaceae (\textit{Theobroma}) and Malvaceae (\textit{Gossypium} and \textit{Thespesia}) are the most highly derived. Elaeocarpaceae was not represented in this broad analysis (their figure 10B).

Alverson et al. (1998) used \textit{rbcL} data for their analysis of the Malvales (represented by 13 genera) and other Rosidae. They found that there is strong support for the monophyly of the core Malvalean families: Bombacaceae, Malvaceae, Sterculiaceae, and Tiliaceae; but members of the Elaeocarpaceae are not closely related to the core families. They found that Malvaceae (represented by \textit{Gossypium} and \textit{Thespesia}) appears to be monophyletic. Malvaceae was placed as the most "advanced" group in the order and was derived from Bombacaceae. There was a paraphyly of the Bombacaceae, Sterculiaceae, and Tiliaceae.

Several cladistic studies have used molecular data to focus on the order Malvales. Alverson et al. (1999) used chloroplast \textit{ndhF} gene sequences; Bayer et al. (1999) used \textit{rbcL} DNA sequences; and Baum, Alverson, and Nyffeler (1998) compiled various forms of molecular data. These analyses concur that Malvaceae s.s. was monophyletic and that the Bombacaceae, Sterculiaceae, and Tiliaceae were nonmonophyletic. In addition, Malvaceae formed a clade with some members of the Bombacaceae.
Judd and Manchester (1997) performed a cladistic analysis of the Malvales (represented by 46 genera) using morphological, anatomical, palynological, and chemical characters. They also found that Tiliaceae, Sterculiaceae, and Bombacaceae are paraphyletic and that Malvaceae is likely monophyletic. Their analysis places Tiliaceae as most basal within the four core Malvales and Malvaceae as the most advanced; with Malvaceae and Bombacaceae together forming a clade.

**Taxonomic history of Malvaceae** -- Opinions differ as to where to draw the lines between species, between genera, and between tribes in the Malvaceae (Kearney, 1951; Hutchinson, 1967). Early treatments of the family were described by Baillon (1875), Maout and Decaisne (1876), Schumann (1891), Edlin (1935), Kearney (1951), Benson (1957), and Engler (1964). Edlin (1935) moved the Hibisceae (which included *Howittia*) and Kydieae (*Kydia*) tribes to the Bombacaceae so that Malvaceae included only schizocarpous fruits. Kearney (1951) reevaluated the American genera of Malvaceae and recognized four tribes, Hibisceae, Ureneae, Malopeae, and Malveae. The Malveae was further subdivided into the subtribes Corynabutilinae, Malvinae, Abutilinae, and Sidinae. The major difference from Kearney's (1951) treatment and Hutchinson's (1967) is the addition of Old World genera. In addition, he removed two subtribes, Abutilinae and Sidinae, from Malveae and placed them into a fifth tribe called Abutileae. Bates (1968) studied the Malveae and claimed the earlier systems overemphasized a few key characters, mainly gynoecial characters, and suggested a system based largely on a number of correlated characters from morphology, cytology, and phytogeography. He combined Malopeae into Malveae and therefore recognized three major tribes of Malvaceae: Malveae, Hibisceae, and
Ureneae. He also pointed out that Kydia and Howittia do not fall easily into any one tribe as currently defined. Bates (1968) and Bates and Blanchard (1970) further subdivided Malveae into informal groups called "alliances". In 1968, Fryxell resurrected and redefined the tribe Gossypieae, separating it from the Hibisceae. In 1975, Fryxell removed the genus Decaschistia from Hibisceae and placed the genus in a tribe of its own, Decaschistieae. Fryxell (1988) resurrected the older name Malvavisceae for the tribe otherwise known as Ureneae or Pavonieae. Subsequently, the genera included in the Malvavisceae, in particular Pavonia, were redefined (Fryxell, 1999). A recent description of the American genera of Malvaceae by Fryxell (1997) takes into account more than 20 new genera since Kearney's (1951) treatment and numerous revisions, expansions, narrowings, and reinterpretations of existing genera.

Thus, the five currently recognized tribes in Malvaceae are Gossypieae, Hibisceae, Malvavisceae, Malveae, and Decaschistieae. Major characteristic of the tribes are summarized in Table 1.2. Some of the genera with questionable placement in a tribe or in the family include: Montezuma (now included in Thespesia), Hampea, Camptostemon, Papuodendron, Durio, Bastardia, Bastardiopsis, Cephalohibiscus, Howittia, and Kydia (Bates, 1968; Fryxell, 1968, 1969). Both the Gossypieae and Hibisceae show affinities to the Bombacaceae (Fryxell, 1968).

**Phylogeny of the tribes** -- Hutchinson (1967) postulated that the most primitive tribe to be Malopeae (now included in the Malveae) because of the arrangement of the numerous carpels characteristic of the tribe. He also speculated that Ureneae (now Malvavisceae) was probably the most recently evolved tribe due to "splitting (chorisis) of the styles" to yield style branches
TABLE 1.2. Comparison of tribes of Malvaceae.

<table>
<thead>
<tr>
<th>Characteristic</th>
<th>Gossypieae</th>
<th>Hibisceae</th>
<th>Malvavisceae</th>
<th>Malveae</th>
<th>Decaschistieae</th>
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</thead>
<tbody>
<tr>
<td>Fruit</td>
<td>capsule</td>
<td>capsule</td>
<td>schizocarp</td>
<td>schizocarp</td>
<td>capsule</td>
</tr>
<tr>
<td>Carpels per fruit</td>
<td>3-5</td>
<td>5</td>
<td>5</td>
<td>3-∞</td>
<td>10 (or fewer)</td>
</tr>
<tr>
<td>Styles</td>
<td>connate,</td>
<td>free, 5</td>
<td>free, 10</td>
<td>free, 3-∞</td>
<td>free, 10</td>
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<td></td>
<td>stigma lobes 3-5</td>
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<td>Stigmas per mericarp</td>
<td>1</td>
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<td>2</td>
<td>1</td>
<td>1</td>
</tr>
<tr>
<td>Apex of staminal column</td>
<td>5-toothed</td>
<td>5-toothed</td>
<td>5-toothed</td>
<td>antheriferous</td>
<td>5-toothed (no teeth)</td>
</tr>
<tr>
<td>Gossypol glands</td>
<td>present</td>
<td>absent</td>
<td>absent</td>
<td>absent</td>
<td>absent</td>
</tr>
<tr>
<td>Foliar nectaries</td>
<td>present</td>
<td>absent</td>
<td>absent</td>
<td>absent</td>
<td>present</td>
</tr>
<tr>
<td></td>
<td>in most</td>
<td>(present in 1 genus)</td>
<td>(present in 1 genus)</td>
<td></td>
<td></td>
</tr>
<tr>
<td>Involucellar nectaries</td>
<td>present</td>
<td>absent</td>
<td>absent</td>
<td>absent</td>
<td>absent</td>
</tr>
</tbody>
</table>

twice as numerous as the carpels. It should be noted, however, that in the Malvavisceae each gynoecium is comprised of ten carpels (Payer, 1857; Saunders, 1936; van Heel, 1978).

Bates (1968), with his three-tribe system, stated that "The phylogenetic relationship of the tribes cannot be determined at present, but there is no compelling reason to believe that any of the three is ancestral to another." He concluded that the tribes had a common ancestry, that divergence probably occurred early in the family history, and that each tribe may be considered to have had a long and distinct evolutionary history. His theory was supported by the widespread distribution and by the diversity of morphological and cytological forms comprising each tribe.

Based on pollen morphology, Christensen (1986) concluded that tribal divergence probably occurred early in the history of the family. Using Hutchinson’s 1967 tribal divisions, Christensen theorized that Malveae (including Malopeae) and Abutileae had a long and distinct evolutionary history. He stated that Hibisceae and Ureneae should be regarded as very close to one another.

Fryxell and La Duke (1994, *abstract only*) produced their cladistic analysis of approximately 70% of the genera in Malvaceae using morphological characters. In this analysis, Malveae is bifurcated into two large subgroups. Previously proposed subdivisions of this tribe were supported to varying degrees. Malvavisceae and Gossypieae clades were maintained. Genera placed in the Hibisceae were intact to a lesser extent. They stated that: "Placements of genera such as *Kydia*, *Abelmoschus*, *Wercklea*, *Kosteletzkya*, *Sida*, *Abutilon*, and *Billieturnera* are of special interest."
Publication of this analysis by Fryxell and La Duke with more details about these taxa, hopefully in the near future, are anticipated.

La Duke and Doebley (1995) used chloroplast DNA restriction site mapping of 23 genera to elucidate phylogenetic relationships. In their analysis, Malvaceae was divided into two main subgroups. Members of Malveae formed a monophyletic group, with the Abutilon alliance forming a sister group to the remainder of the Malveae. Other alliances within the tribe did not form monophyletic groups. Members of Gossypieae also formed a monophyletic group, but members of Malvavisceae and Hibisceae did not form monophyletic groups. Genera that were previously mentioned as being in questionable placement in the tribe or in the family were not included in the study by La Duke and Doebley.

Judd and Manchester (1997) found that the commonly recognized tribes Malvavisceae (represented by Urena and Malvaviscus) and Malveae (represented by Sida, Sphaeralcea, and Abutilon) were tentatively supported; the tribes Hibisceae and Gossypieae each had only one representative and Decaschistieae was not included in their analysis. Gossypieae (represented by Thespesia) was positioned basally in Malvaceae, and Hibisceae (represented by Hibiscus) was positioned as the sister group to the more advanced Malveae + Malvavisceae.

The study by Alverson et al. (1998) did not extensively sample the core malvalean families; therefore, valid conclusions about the relationships within Malvaceae can not be made from their analysis. In the study by Alverson et al. (1999) the Gossypieae were monophyletic and part of a clade with members of the Malveae. The two representatives of Malvavisceae were closely related and part of a clade with one Hibisceae representative.
Camptostemon, which has affinities to both the Bombacaceae and Malvaceae, formed a larger clade with the Malvaceae.

**Previous work on floral development** -- Early research on Malvaceae floral development was done by Payer (1857). He examined *Malvaviscus arborea, Lavatera olbia, Abelmoschus moscheutos, Hibiscus ilicifolius, Modiola caroliniana, Sphaeralcea angustifolia, Pavonia hastata, Urena lobata, Kitaibelia vitifolia, Malva rotundifolia, and Malope trifida*. His illustrations show various stages of floral development, but a complete ontogenetic series was not done for any of the taxa.

Very little recent research (with the possible exception of that on *Gossypium*) has dealt with floral development in the Malvaceae. Saunders (1936) examined the vasculature of several genera in Hibisceae, Ureneae, Malopeae, and Malveae. Rao (1952) used serial microtome sections to study the vasculature in Malvales. Van Heel studied the androecium of Malvales (1966) and the development of the pistil in the Ureneae (Malvavisceae) (1978) using microtome sections, clearings, and whole mounts with a light microscope. He did not do complete developmental series of the taxa. Sattler (1973) described floral ontogeny of two taxa (*Malva neglecta* and *Althaea rosea*) in Malveae, based on a technique of acid fuchsin staining of whole mounts immersed and photographed with dipping cones on a light microscope.

Moncur (1981) used scanning electron microscopy (SEM) to show partial ontogeny in *Gossypium hirsutum* and *Hibiscus cannabinus*. Ault (1987), examined the floral ontogeny in *Hibiscus acutosella* using SEM and paraffin sections. Endress (1994) used SEM to look at a few sporadic stages of *Kitaibelia vitifolia* (stamens), and *Pavonia hastata* (chasmogamy and
oleistogamy), and *Abutilon megapotamicum* (nectary). Van Heel (1995) examined the morphology of the gynoecia in *Kitaibelis vitifolia* and *Malope trifida*. In summary, complete floral ontogenies, using a uniform technique, are available for only one or two malvaceous taxa. A broad comparative survey, as planned here, is urgently needed. Complete floral ontogenies of many taxa are needed to fill in some of the information gaps on how the flowers initiate and to help clarify confusing and often conflicting descriptions given in previous literature. This information will help to test the morphologically based tribal affiliations, elucidate phylogeny, and complement current molecular research.

In addition, little research has been done on floral development in the outgroups. I have selected *Sterculia ceramica* and *Herrania sp.* in Sterculiaceae and *Pachira aquatica* in Bombacaceae for cladistic analysis. Selection of these families as outgroups is based in part on the cladistic analysis by Chase et al. (1993) in which Sterculiaceae was found to be the closest outgroup to Malvaceae and Bombacaceae was found to be the most primitive in the order. Judd and Manchester (1997) and Alverson et al. (1998, 1999) found in their analyses that Malvaceae was more closely allied with Bombacaceae and that Sterculiaceae and Tiliaceae were more basal. In addition, Fryxell (1968) described how some members of Malvaceae show affinities to Bombacaceae. Since both Bombacaceae and Sterculiaceae have been indicated as closely related to the Malvaceae, I chose representatives of both families as outgroups. For the cladistic analysis, it is necessary to document floral ontogenies for the outgroup taxa as well as selected taxa in Malvaceae.
OBJECTIVES OF PROJECT

I propose to compare floral development in the Malvaceae. In this study, I hope to address many questions concerning development and ontogeny in the family. In addition, this study will use ontogenetic characters to characterize the tribes and to set up a basic framework that can be used to help determine the taxonomic position of some of the problem taxa. A cladistic analysis using developmental and conventional morphological characters will also be produced to determine the evolutionary relationships among the tribes and some of the genera within Malvaceae.

Floral ontogeny -- Since complete floral developmental studies are lacking for Malvaceae, one major purpose of this research is to compare floral ontogeny in representatives of the Malvaceae. Scanning electron microscopy will be used to discover the sequence of initiation, pattern of initiation within a whorl (simultaneous, unidirectional, spiral, etc.), orientation of organs, carpel arrangement, and pattern of stamen proliferation in selected genera. Comparisons will be made of the floral organ initiation within and among the tribes of Malvaceae (excluding Decaschistieae).

Morphological questions -- Another major purpose of this study is to address many questions concerning floral development and floral ontogeny in the family. For example, it is unclear if a common (i.e. shared) ring meristem (an unusual developmental feature among angiosperms) forms in any of the representatives of Malvaceae. Payer (1857) and van Heel (1966) alluded to the possible presence of a common petal-stamen ring meristem. Sattler (1973), however, interpreted malvaceous petal initiation as involving distinct primordia without any ring, and with adnation to the androecium occurring later. My analysis will determine generic and tribal distribution of this ring
meristem and whether the meristem ring differs in presence and in character among taxa and between tribes.

A second developmental issue addressed in this study is to examine the mode of proliferation of stamen number in the different genera (and tribes) and to link different initiation patterns to anther divergence from the staminal column. The anthers can diverge singly, in pairs, or in more complex patterns (van Heel, 1966).

A third morphological objective is to study the development, or lack of development, of sterile teeth in Malvaceae. Staminal columns of four of the tribes of Malvaceae have sterile teeth at the apex. The Malveae lacks sterile teeth (Fryxell, 1988). I will determine whether some of the taxa that lack teeth at maturity actually initiate the primordia but suppress further development of the organs.

The descriptions of carpel development for many of the genera vary as to whether they initiate as one discrete whorl, as two whorls, or as randomly scattered carpels (Bates, 1968; van Heel, 1978). Sattler (1973) also suggested the formation of a carpel "rim" in some taxa. Therefore, another focus of this research is to further investigate and to compare carpel initiation in representative taxa of the family Malvaceae.

In addition, it is unclear how the gynoecium develops in the Malvavisceae. Taxa placed in this tribe have a gynoecium with ten styles and stigmas but only a five-locular ovary. According to van Heel (1978), ten carpels initiate as two whorls of five; he concluded that the last-formed set of five carpels is sterile. Depending on the taxon, the sterile carpel primordia either do not form locules or, if locules are formed, they do not develop further (Saunders, 1936; van Heel, 1978). More floral studies are needed to
determine if the sterile set of carpels is always the last to form and to
determine how the sterile carpel locules are suppressed in various taxa in the
tribe.

**Taxonomic position** -- This study is also intended to lend some insight
into the position of questionable genera within a tribe or even within the family. Currently, opinions differ as to where to draw the line between species, between genera, and between tribes of the Malvaceae. Even definition of the family in the Malvales has been disputed. Ontogeny will be used to characterize the tribes and to set up a basic framework that can be used for future research to determine the taxonomic position of some of the problem genera.

**Phylogeny** -- Since there are discrepancies in the phylogenetic analyses that have been done so far, a major objective of this project is to determine the phylogeny of Malvaceae using floral ontogeny in addition to diagnostic morphological characters such as merosity, connation, adnation, style type, nectary type, habit, leaf shape, fruit type, etc. A cladistic analysis will be performed using PAUP and McClade algorithms in order to investigate the evolutionary relationships among the tribes (or genera) of the family.

**DATA COLLECTION AND ANALYSIS**

**Materials** -- Floral material was obtained from as many genera and species as possible in the Malvaceae. Efforts were made to obtain a representative sample of at least three genera in each of the tribes (with the exception of Decaschistieae which is monotypic). Natural populations were favored over cultivars and, when possible, more than one population of plants was examined for a species. In addition, selected taxa from closely related families in Malvales were also collected.
The taxa that were used in this project were chosen for several reasons. A species of the type genus of each tribe (excluding Decaschistieae, which was unavailable) was examined, in addition to species of as many additional genera as possible in the tribe, to assure representative sampling. When possible, a combination of both temperate and tropical taxa from different global locations was chosen to give the broadest representation of the family. Taxa that are in questionable position in a tribe or in the family will be examined in future projects.

For comparative purposes, outgroups are important in cladistic analyses. The most important outgroup is the sister group (Wiley, et al., 1991). According to the analysis by Chase, et al. (1993, their figure 10B), Sterculiaceae is the sister group to Malvaceae; closely allied are the families Tiliaceae and Bombacaceae, with Bombacaceae being the more basal of the clade. Based on morphological characters, some members of Malvaceae show affinities to the Bombacaceae (Fryxell, 1968). Therefore, in my analysis, I chose to use two representatives of genera in Sterculiaceae and one representative of a genus in Bombacaceae. Again, availability of material was a limiting factor in the selection. A complete list of taxa examined in this research can be found in Table 6.1 (page 491) and Table 7.1 (page 527).

Methods -- Floral buds at various developmental stages were collected and fixed in formalin-acetic acid-alcohol (FAA) [(90 ml 70% ethanol (CH₃CH₂OH), 5 ml glacial acetic acid (CH₃COOH), 5 ml formalin (37% HCHO)] for at least 48 hours. Prior to dissection, the buds were transferred through two to four changes of 95% ethanol, then dissected in 95% ethanol. Material was dehydrated in 100% ethanol and critical point dried in a Denton DCP-1 with liquid CO₂. Specimens were mounted on aluminum stubs with
Avery press-on Spot-O-Glue and sputter-coated with gold-palladium in an Edwards S-150 apparatus. Micrographs were taken using a Cambridge S-260 SEM at 15 kV and spot size 6. Kodak Tri-X (TXT4164) sheet film was used. The micrographs were arranged in chronological order, and selected representatives of successive stages were assembled as plates showing floral ontogeny for each representative species.

Information obtained about floral development in a species was converted to discrete characters and placed in a matrix that was used in cladistic analyses using McClade and PAUP algorithms. Reproductive and vegetative characters for the phylogenetic analysis were obtained from material preserved in 95% ethanol, herbarium specimens, and a literature search.

**LITERATURE CITED**


CHAPTER 2
FLORAL ONTOGENY IN THE TRIBE MALVAVISCEAE WITH SPECIAL EMPHASIS ON GYNOECIAL DEVELOPMENT

INTRODUCTION

Malvavisceae K. Presl, Reliq. Haenk. is one of five tribes that Fryxell (1975, 1988) recognized in his treatment of the Malvaceae family. The tribe was formerly known as Ureneae Bentham & Hooker in earlier treatments by Kearney (1951) and Hutchinson (1967). Currently, there are eight genera in the tribe: *Anotea, Malachra, Malvaviscus, Pavonia, Peltaea, Urena, Phragmocarpidium*, and *Rojasimalva*. The large genus *Pavonia* now encompasses the former genera *Blanchetiastrum, Codonochlamys, Goethea, Lopimia*, and *Triplochlamys* (Fryxell, 1999).

In general, malvaceous flowers are solitary or fasciculate in leaf axils or grouped in inflorescences (racemes, panicles, spikes, scorpioid cymes, or rarely umbels or heads). They are usually pentamerous, polysymmetric, and bisexual with an involucel or involucre, a monadelphous androecium, and a superior gynoecium. Anthers are bisporangiate and monothecal (contain only two pollen sacs). Pollen is typically spheroidal and echinate. Fruits are capsules, schizocarps, or berries (Cronquist, 1981; Fryxell, 1988).

Members of the tribe Malvavisceae are distinguished primarily by having two styles per mericarp (each mericarp equals a segment with a locular cavity in the schizocarp). All other Malvaceae have a one-to-one ratio of styles per mericarp. Other features that in combination delineate the tribe are: five mericarps in the schizocarpous fruit, five-toothed apex of the staminal
column, ten free styles in the gynoecium, and the absence of gossypol glands (Fryxell, 1975, 1988).

One purpose of this project is to make a comprehensive study of floral ontogeny in the tribe Malvavisceae using scanning electron microscopy (SEM). Very little recent research on floral development has dealt with Malvaceae (with the possible exception of *Gossypium*). Previous studies that dealt with floral development in the Malvavisceae have used light microscopy techniques. Payer (1857) looked at various stages of floral development. Saunders (1936) and Rao (1952) described the vascular system, and van Heel (1966) examined the androecium and (1978) development of the pistil. These studies did not include complete developmental series of the flowers.

Another purpose of this research is to add insight through a knowledge of development to the many unusual structural features in flowers of Malvavisceae. One puzzle involves the ovary that is composed of five apparent carpels but has ten stylar components. Payer (1857), Saunders (1936), and van Heel (1978) demonstrated that ten carpel primordia initiate, but five are aborted or suppressed in some way. In many cases, the literature was unclear or contradictory on the position of the locules relative to petal and sepal positions. In addition, van Heel (1978) stated that the carpels in Ureneae (Malvavisceae) initiate as two whorls but that it is difficult to distinguish the inner from the outer whorl. In studies of other members of the Malvaceae, the carpels may initiate either in a single whorl (Sattler, 1973) or common primordia may produce the carpels (Endress, 1981; Sattler, 1973). This study will try to clarify the diversity of the differing patterns and positions of carpel initiation.
Another structural anomaly in flowers of this family is the fused multistaminate androecium. Little is known about how the stamens and petals initiate in this family. Accounts of androecial development have been very general; no studies have shown a complete detailed ontogenetic series for development of each of the many sets of stamens. In one interpretation, van Heel (1966) described a "peripheral wall" created by a central depression in the floral apex. On this wall, five regions originate that develop into "staminal buttresses"; subsequently, stamen primordia are said to originate on these buttresses in centrifugal succession. Petals initiate outward from these buttresses. Sattler (1973) depicted two members of the Malveae as having petals that initiate as distinct primordia, with adnation to the androecial column occurring later. In *Malva neglecta*, he characterized the androecium appearing first as a ridge, then primordia developing. In *Alcea rosea*, he reported five androecial primordia initiating first, then interprimordial growth creating an almost "girdling androecial primordium". In both these taxa, Sattler described "primary" (common) stamen primordia, with subsequent proliferation occurring laterally and centrifugally. Endress (1994) briefly described the occurrence of secondary polyandry (secondary subdivision of the primary androecial primordia) in *Kitaibelia vitifolia* (Malveae). With the exception of van Heel (1966), none of these studies alluded to the possible presence of a petal-stamen ring meristem or of common petal-stamen primordia. This study will try to determine the detailed patterns of stamen proliferation and the nature of the association between the petals and the androecium in representative taxa.

A final aspect of this paper is to characterize the Malvavisceae using ontogenetic characters. This research is part of a larger study to characterize
and compare the tribes of Malvaceae and to use ontogenetic characters as well as morphological characters to determine the phylogeny of the tribes and genera. Tribes of Malvaceae have changed in content over the years, depending on the researcher. Comparative floral development can elucidate systematic differences among taxa. The overall aim of this study is to use scanning electron microscopy to compare floral development in representative examples of the tribes of Malvaceae, to test the validity of current tribal assignments.

**MATERIALS AND METHODS**

Floral material was collected for six taxa (*Malachra capitata*, *Malvaviscus arboreus var. drummondii*, *Pavonia bahamensis*, *Pavonia spinifex*, *Pavonia strictiflora* = *Goethea strictiflora*, and *Urena lobata*) from various sources (Table 2.1). When possible, herbarium vouchers were made and retained by the author. Floral buds of various developmental stages were collected and fixed in formalin-acetic acid-alcohol (FAA). Prior to dissection, buds were transferred through two to four changes of 95% ethanol, then dissected in 95% ethanol. Material was dehydrated in 100% ethanol and critical point dried in a Denton DCP-1 with liquid CO₂. Specimens were mounted on aluminum stubs with Avery press-on Spot-O-Glue and sputter-coated with gold-palladium in an Edwards S-150 apparatus. Micrographs were taken using a Cambridge S-260 scanning electron microscope at 15 kV and spot size 6. Kodak Tri-X (TXT 4164) sheet film was used.

Fairly complete ontogenetic series were obtained for all taxa except *Pavonia spinifex*. A complete developmental series will be presented in this paper for *Malvaviscus arboreus*. For the sake of brevity, only selected stages of development will be presented for the other taxa. Special emphasis will be
TABLE 2.1. Sources of Malvavisceae plant material and voucher information for taxa examined in this floral study.

<table>
<thead>
<tr>
<th>Taxon</th>
<th>Voucher</th>
<th>Source, collector, and date</th>
</tr>
</thead>
<tbody>
<tr>
<td>Malachra capitata L.</td>
<td>TSC-0127, 0144 - 0146</td>
<td>Greenhouse at Univ. of N. Dakota, Grand Forks, ND, US, (Fryxell # 5038, origin - Victoria Co., TX, US), J. La Duke, Oct., 1993; Herbarium material courtesy Fryxell's collection at Univ. of Texas, Austin, TX, US: Coalcomán, Michoacán, Mexico, G.B. Hinton et al. #12154 (LL), Sept., 1938; Hidalgo Co., TX, US, Correll and Schweinfurth 15644 (LL) April, 1957; Brownsville, TX, US, Runyon 3939 (TEX), Nov., 1944</td>
</tr>
<tr>
<td>Urena lobata L.</td>
<td>TSC-0107</td>
<td>Weed in Miami, FL, US, T. Crozier with K. Kantz, June, 1993</td>
</tr>
</tbody>
</table>
given to stages that are important for comparison or that differ from *M. arboreus*.

Some late stage floral characters were obtained by examining herbarium vouchers and FAA-ethanol preserved material with Nikon dissecting and light microscopes. In some instances, literature was used to verify and complete mature floral descriptions.

**Terminology** -- In Malvaceae literature, the terms *involucel* and *involucre* (and the accompanying terms *epicalyx*, *bracts*, and *bractlets*) are sometimes confused, but generally describe the specialized elements that subtend either an individual flower or an inflorescence, respectively. Fryxell (1988) uses the term *floral bracts* to describe the specialized elements that subtend a group of flowers or occur at the base of the pedicel of a single flower. He refers to the specialized elements that immediately subtend the calyx as an *involucel* or as *bractlets* or *involucellar bracts*. This author, in staying with Fryxell's terminology, further defines the terms from an ontogenetic standpoint. *Floral bracts* are specialized appendages that are often associated with floral apices, but do not actually initiate on the floral apices; they initiate as separate mounds near the floral apices. *Bractlets* (*involucellar bracts* or collectively an *involucel*) are used to define the specialized appendages that initiate on a floral apex and precede the calyx. These bractlets may be positioned in the mature flower either adjacent to the calyx on the receptacle or spaced along the pedicel.

In keeping with Fryxell's (1988) terminology, *pedicel* refers to the stalk that bears an individual flower. *Peduncle* refers to a stalk that bears a group of flowers. In the case of an uniflorate inflorescence, on an often articulated stalk, the term *pedicel* is preferred.
Davis and Selvaraj (1964) delineated the terms used to describe petal contortion in Malvaceae. A corolla is contorted to the left (clockwise aestivation) if when viewed apically, the inner margins of the petals curve in a clockwise direction towards the periphery, and a corolla is contorted to the right (counter-clockwise aestivation) if the inner margins of the petals curve in a counter-clockwise direction towards the periphery.

Order of initiation of floral organs can be described as unidirectional, bidirectional, simultaneous, spiral, or helical. The latter three occur among malvaceous flowers. Simultaneous initiation refers to organs that initiate at the same time (synchronously). The terms spiral and helical are often used interchangeably in the literature, but I prefer to distinguish between the two. In a spiral pattern, initiation of primordia winds around the floral apex and gradually recedes from or approaches the apex. This term (as used for Malvaceae) can also apply to initiation of flowers within an inflorescence. In a helical pattern, initiation of primordia in a whorl generally follow a 2/5 phyllotaxy, with the first and second primordia usually initiating on nearly opposite sides of the apex. With helical initiation the primordia are equidistant from a central axis and unless stated otherwise, occur at the same level around the apical meristem.

In referring to stamens and carpels, a set of primordia consist of identical (same type) primordia that have initiated at the same time and thus have been given the same initiation numbers. For example, if the androecium initially consists of five common stamen primordia (or mounds) that initiated simultaneously, these would be designated as the first set and each mound would be a numbered 1. If subsequently five more mounds initiate laterally to each of the first primordia, then these five new mounds would constitute the
second set and each would be numbered 2. On the micrographs, usually only one or two of the primordia in each set have been labeled.

The terms sectorial region and sectorial organ group are used to describe a cluster of stamen primordia (or petal and stamen primordia) that initiate from a common area or mound on the petal-stamen ring meristem. The clustered stamen primordia that constitute a sectorial region are numbered 1 - 3+ (i.e. one stamen from each set that initiates).

A ring meristem describes a meristematic rim or ring of tissue on the floral apex that is set apart from the rest of the floral apex (either by a trough separating it from the remaining raised central portion of the apex or by a central depression in the remaining floral apex). This ring is capable of producing a whorl or whorls of organs. This ring may be mounded, flat, or sloped.

I use the term common stamen primordia for any androecial structures that will divide again, and the term stamen primordia for the final structures that do not redivide. The numbers placed on the androecial structures reflect the chronological sequence of initiation; not whether the structures are or are not common stamen primordia. For example, the structures numbered 1 (or first) are the first common stamen primordia to appear, but they keep the same numbers as they subdivide and become stamen primordia.

RESULTS

Malaviscus arboreus var. Drummondii -- Organography -- The plants are shrublets to shrubs with flowers solitary or several in each leaf axil. The mature flowers are tubular in shape and positioned upright. The involucel consists of 7 to 12 linear to spatulate green bractlets. The calyx is green, campanulate, and five-lobed. The corolla is tubular and contorted. The five
red petals are erect, obovate to cuneate, auriculate at the base, and spread (flare) only at the apex. Twenty-five stamens are fused into an exserted androecial column with five apical teeth. Short, retrorse filaments diverge towards the apex of the column. The gynoecial column is exserted and terminated by ten styles and stigmas. The red (sometimes white-colored) fruit is a five-celled baccate schizocarp (or berry) that is indehiscent. Each locule contains only one seed (observations of collected material; Correll and Johnston, 1979; Turner and Mendenhall, 1993).

**Initiation and early development of the involucel and perianth** -- The floral apices initiate in the axils of leaf primordia (Fig. 2.1). All of the 7 to 12 involucellar bracts initiate on a low ring on the floral apex before any sepal primordia appear. The sequential order of bractlet initiation is unclear, but it possibly is helical (Fig. 2.1); there is a high degree of modification and variability among flowers. The pre-sepal apex is relatively flat (Fig. 2.2), and it becomes multi-sided in accordance with the number of surrounding bractlets (Fig. 2.3). A very low (not well-defined) ring meristem develops along the periphery of the apex (Fig. 2.3). On this ring, the five sepals initiate in helical order. The first two sepals appear to initiate at nearly the same time on opposite sides of the apex (Fig. 2.3). This is followed by initiation of three other sepal primordia in the same whorl (Fig. 2.4). The sepals are fused at the base from early development and as organ enlargement begins, they equalize in size, and trichomes initiate (Fig. 2.5).

The pre-petal apex also starts off relatively flat, but is pentagonal in outline (Fig. 2.6). Then a pronounced ring meristem forms (Figs. 2.7, 2.8). Five common petal-stamen mounds (partitions or sectorial regions) form simultaneously on the ring (Fig. 2.8). These mounds alternate with the sepals.
and will subdivide into primordia of petals and stamens. A petal primordium initiates on the lower, abaxial perimeter of each of the five common petal-stamen primordia (Fig. 2.9). Petal initiation of all five is simultaneous. The five petal primordia are alternate to the sepals but slightly off-center to each; i.e., the petal primordium is initially on a radius slightly to the right or left of the related common stamen primordium (Fig. 2.9). Position of the petal primordia is the first indication of whether the corolla of an individual flower will twist clockwise or counterclockwise. As the petal primordium broadens (or begins to grow marginally), it becomes asymmetric; the highest part of each primordium is nearest its related major common stamen primordium and nearest the gap between two sepals (Figs. 2.10, 2.11). The taller side of the petal primordium will be on the outside of the contorted corolla; the shorter side will be overlapped by one adjacent petal. The flower petal primordia in the buds in Figs. 2.10, 2.12, and 2.13 will contort to the left or clockwise; those shown in Figs. 2.11, 2.14, and 2.15 will contort to the right or counterclockwise. Even with further development, the center of the petal blade remains slightly off-center between the sepals (Fig. 2.13).

Initiation and early development of the androecium -- The first five common stamen primordia broaden slightly (Fig. 2.10). The direction of this broadening matches the direction of the petal contortion: if petals overlap to the left, the common stamen primordia also expand to the left (Fig. 2.10); if the petals overlap to the right, the common stamen primordia expand to the right (Figs. 2.11, 2.16). More simply, each of the original stamen primordia broadens unequally. From each of the five first common stamen primordia, a second, smaller mound becomes distinct to one side of the first, in the appropriate lateral direction (Figs. 2.11, 2.16). The two adjacent common
stamen primordia (designated 1 and 2) are both opposite the corresponding petal blade (Fig. 2.11). The first five common stamen primordia (i.e. the first set) then elongate centrifugally (Fig. 2.11) and initiate a third set of five stamen primordia to the outside (Figs. 2.12, 2.13, 2.17). The first and second sets of common stamen primordia then elongate centripetally (Figs. 2.13, 2.14) and become "peanut-shaped" (Fig. 2.15). The first set of common stamen primordia bifurcates to yield the fourth set of five stamen primordia at approximately the same time as the second set bifurcates to form the fifth set of five stamen primordia (Fig. 2.18). Note that the bifurcation of common primordia initially yields unequal-sized lobes or lopsided "peanuts" (Fig. 2.15). Within each set of five stamen primordia, initiation is simultaneous. At this point, each of these 25 primordia will become a stamen and therefore can be considered as an individual stamen primordium (Figs. 2.19, 2.21). A ring of tissue from the inner part of the ring meristem persists after stamen initiation (Figs. 2.12, 2.13, 2.20). The inner surface of the ring becomes pentagonal in outline, with the sides of the pentagon parallel to the petal blades (Fig. 2.20). After all the stamen primordia have initiated, this remaining ring tissue forms five mounds (interior to and alternate to the fourth set of stamen primordia, essentially opposite but off-center to the petals) on the inner periphery of the ring (Fig. 2.21). As the androecial column elongates, these mound primordia grow upward as a tube and form the inner wall of the androecial column (Fig. 2.22) and subsequently develop into the five sterile teeth at the top of the column (Fig. 2.19).

Initiation and early development of the gynoecium -- Carpel initiation overlaps part of stamen initiation in time. The first five carpel primordia are initiated when the first and second sets of common stamen primordia are
elongating, before the fourth and fifth sets of stamen primordia become distinct. These five carpel primordia initiate simultaneously and opposite the first set of common stamen primordia which are elongating to form the fourth set of stamen primordia. These carpel primordia alternate with the remaining ring tissue that will become the sterile andro-teeth in the corners of the pentagon (Figs. 2.20, 2.21). Carpels of the first set generally appear to alternate with the petals. Initially, there are spaces on the meristem between these five carpels (Fig. 2.21). As the androecial column begins to elongate upward, this tissue between the first carpel primordia begins to mound up (Fig. 2.22) so that a second set of five carpels is initiated in the spaces between members of the first set. Initiation of this second set of carpel primordia is simultaneous. Thus, ten carpel primordia are initiated in two initiation events as two separate sets (or whorls) of five. Both sets are equidistant from the central floral axis and appear to share the same "spatial whorl".

Only carpels of the second set of primordia form locular cavities; the first set of carpel primordia shows no signs of cavity formation (Figs. 2.23, 2.24). Locule formation occurs at about the time anthers and filaments are differentiating. The fertile carpel primordial tips grow upward and inward towards the center of the column while the bases remain peripheral. The sides of the cavities appear to be formed mostly by the growth of adjacent sterile carpels, which at their bases grow inward towards the center of the column (Figs. 2.24 - 2.27). At this stage, the sterile carpels (first-formed set) are taller than the fertile carpels. The ovules begin to form (Fig. 2.27) before the styles appear. One ovule forms in each of the five locules. Fusion at the base of the ovary is so complete that it is difficult to distinguish one carpel wall from another (Figs. 2.27 - 2.31). As carpels develop, differences in height and
position of the two carpel sets become more pronounced. The styles of the sterile carpels are taller and occupy the center of the column; styles of the fertile carpels are shorter and more peripheral (Figs. 2.29, 2.30). Residual meristem remains in the center of the floral apex and is not initially incorporated into the gynoecial primordia. This tissue forms a mound as the gynoecium develops around it (Figs. 2.26, 2.27, 2.31).

**Midstage and mature reproductive characters** -- The bractlets of the involucel remain separated from each other and immediately subtend the calyx; i.e. they are on the receptacle. The sepals fuse into a tube and, through part of their development, form a protective dome over the bud, and therefore appear to serve as the main source of protection for the subsequently initiating organ primordia. At maturity, the sepals are fused a little more than half their length. Numerous nectarial trichomes form at the base on the inner side of the sepals (Fig. 2.35). The petals are attached to the base of the androecium (Figs. 2.33, 2.35). They are auriculate near the base on only one side, the side that is overlapped by an adjacent petal. The mature corolla is tube-like or funnelform, spreading only at the apex. The petals are usually two to four times the length of the calyx.

Anther differentiation appears in most cases to occur simultaneously although there is some lag in differentiation for primordia that were initiated very late on the column (Figs. 2.23, 2.32, 2.33). The distal portion of each stamen primordium enlarges and an indentation forms between the two microsporangial regions; this occurs between the time of fertile-carpel initiation and cavity formation (Figs. 2.22, 2.23). The anthers are well formed before the filaments begin to elongate (Fig. 2.34). When the filaments do elongate, they become retrorse (Fig. 2.35) and diverge individually from the column.
At maturity, the androecial column is long-exserted, with the anthers attached on the upper fifth of the column due to greater elongation at the base. The anthers are radially displayed around the column. They dehisce by longitudinal slits at the sutures between the two sporangia, opening each sporangium where they were attached to each other. Each of the five sterile teeth at the top of the column becomes terete (circular in cross section) in early development (Figs. 2.33, 2.34), then marginally enlarges to form a flat blade or lamina (Fig. 2.35). These teeth are opposite each of the petals (Figs. 2.33). At maturity the five teeth are small, narrowly triangular, and distinct.

Initially, the gynoecium lags behind the androecium in elongation (Fig. 2.34). The individual styles are distinguishable their entire length on the outer surface of the column (Fig. 2.34). The stigmas begin to differentiate (apically broaden and develop surface texture) before they surpass in height the sterile teeth of the andro-column (Fig. 2.34, 2.35). All ten styles form emergent, capitate stigmas. Some difference in height between styles from sterile and fertile carpels is still evident. At maturity, the gynoecial column is exserted beyond the corolla and the androecium. The gynoecial column is nearly double the length of the petals. The styles separate from the column only at the apex (upper tenth of the length of the gynoecium).

Both the gynoecial and androecial columns twist along their length in the mature flower. No zygomorphy occurs in the perianth or in the androecial and gynoecial columns. The pollen grains are spheroidal, echinate (the spines long and softly pointed), and polyporate (Fig. 2.36). The fruit is five-locular (Fig. 2.37) and about equal in length and width. One ovule forms in each locule and placentation is axile (Fig. 2.37). It is difficult to distinguish the origin of the tissues in the ovary as originating from the sterile or the fertile carpels.
Figs. 2.1 - 2.9. *Malvaviscus arboreus* var. *Drummondii*, initiation of floral apices, bractlets, sepals, ring meristems, and petals. Bars = 200 μm in 2.1 and 2.3 - 2.9, = 100 μm in 2.2. **2.1.** Order of initiation of floral apices (A) is shown with numbers, beginning with one as the first-initiated. Each flower initiates in the axil of a leaf primordia (L) and an accompanying pair of stipules (sp). Floral apex number 1 has bractlet primordia (Bt) on a low ring meristem. **2.2.** Flat pre-sepal apex (A). **2.3.** Apex is multi-sided in accordance with the number of surrounding bractlets. Low ring meristem with first two sepal primordia (S). **2.4.** Helical sepal initiation. Order of initiation shown with numbers. **2.5.** Sepals equalizing in size. Fusion at base of the whorl shown (at arrows). Trichomes initiate on the sepals. **2.6.** Flat, pentagonal pre-petal apex (A). **2.7.** Formation of ring meristem (R). **2.8.** Oblique view of ring and simultaneous initiation of 5 common petal-stamen mounds (m) on the ring. **2.9.** Petal primordia (P) initiate simultaneously on the lower, abaxial perimeter of each of the five common petal-stamen mounds. The adaxial portions of the common mounds become the first five common stamen primordia (St).
Figs. 2.10 - 2.15. *Malvaviscus arboreus* var. *Drummondii*, proliferation of stamens. Bractlet and sepal whorls have been removed. Note that in Figs. 2.10, 2.12, and 2.13 the corolla will contort to the left (clockwise) and in Figs. 2.11, 2.14, and 2.15 it will contort to the right (counterclockwise). Bars = 200 μm. 2.10. Taller part (long arrow) and shorter part (short arrow) of petal primordium shown. Common stamen primordia broadening in a lateral direction - left in this case. 2.11. Taller part (long arrow) of petal primordia are nearer the initial common stamen primordia (1), the new second set of common stamen primordia (2) are nearer the short side (short arrow) of petal primordia. In this flower, the new primordia formed to the right, correlating with the direction of petal contortion. Note early elongation of the first common stamen primordia in a centrifugal direction. 2.12. Initiation of the third set of stamen primordia (3) external to the first common stamen primordia set. Note distinct ring meristem divides off into sectorial organ groups (petal and stamens 1, 2, 3) that were derived from the same common petal-stamen mound. Remaining inner part of ring meristem is apparent (at arrow R). 2.13. Petal position shown as alternate and slightly off-center with the adjacent sepals. Note gap between two sepals (at arrow). Order of initiation of stamen primordia shown with numbers for one sectorial group. The first and second sets of stamen primordia are starting to elongate centripetally. Remaining inner part of ring meristem shown. 2.14. First and second common stamen primordia elongated and starting to take on the "peanut" shape. 2.15. Centripetal bifurcation of first common stamen primordia set to form the fourth stamen set, and bifurcation of second common stamen set to form the fifth stamen set.
Figs. 2.16 - 2.19. *Malvaviscus arboreus* var. *Drummondii*, diagrams showing proliferation of stamens in a flower with corolla that contorts to the right (counterclockwise). 2.16. Polar view of development of secondary stamen primordia (2) in a lateral direction from the original common stamen primordia (1). The first and second stamen primordia of a sectorial group are opposite their corresponding petal. 2.17. Polar view of centrifugal development of a third set of stamen primordia (3) from the first set. 2.18. Polar view of centripetal development of fourth (4) and fifth (5) sets of stamen primordia from the first and second sets, respectively. 2.19. Side view of partially elongated androecial column showing position of young stamens (order of initiation shown with numbers) and petal blades. Sterile teeth (T) shown at the top of the column.
Figs. 2.20 - 2.25. *Malvaviscus arboreus* var. *Drummondii*, initiation of gynoecium. Bars = 200 µm. 2.20. Simultaneous initiation of first five carpels (two at arrows). Stamen mounds shown in order of initiation with numbers. Note remaining ring tissue (R) that will become the sterile teeth. 2.21. First five carpel primordia (one at arrow) are alternate with the sterile teeth (T). Sterile teeth are opposite the petals. All five sets of stamen primordia have been initiated (order within one sectorial group shown with numbers). 2.22. Simultaneous initiation of a second set of carpels (2) that is alternate to the first set (1) and in the same spatial whorl. Members of the second set of carpel primordia are smaller than the first set at this stage and are opposite the sterile teeth. Some stamen primordia are labeled. 2.23. Stamen primordia are differentiating into anthers (a) and filaments (f). The second set of carpel primordia are forming locular cavities (at arrow). 2.24. Cavity formation (at arrow) in the fertile carpels (fc). Sterile carpels (sc) do not form cavities. 2.25. Further development of the locular cavity in the fertile carpels. Note location of suture line between two sterile teeth (at double arrow) opposite the location of a sterile carpel, which is one member of the first-formed set. Locular cavities (at single arrows) are visible in fertile carpels.
Figs. 2.26 - 2.31. *Malvaviscus arboreus* var. *Drummondii*, development of gynoecial column with ovules. The androecial column has been removed. Bars = 200 μm. 2.26. Polar view of sterile carpels growing inward at the base and fertile carpels that remain towards the periphery. Residual meristematic tissue (r) remains inside the gynoecial column. 2.27. Oblique side view of gynoecium. Several carpel walls have been removed to show developing ovules (o). Fusion of carpels at the base is fairly complete. Residual meristem is mounding up. 2.28. Oblique polar view of gynoecial column. Styles are beginning to differentiate and the ovary is fused at the base. 2.29. Oblique polar view of gynoecium. Sterile carpel styles are taller and are inclined inward at the tip of the column. Fertile carpel styles are shorter and remain more to the periphery of the column. 2.30. Oblique polar view of gynoecium. Differences in height and position of styles of fertile and sterile carpels are more pronounced. Note position of ovules in line with the fertile (second set) carpels. 2.31. Side view of gynoecium partly removed showing exposed ovules and residual apical meristem.
Figs. 2.32 - 2.35. *Malvaviscus arboreus* var. *Drummondii*, midstage and late stage development. Bractlets and sepals have been removed. Bars = 500 μm. 2.32. Oblique view of flower showing differentiation of anthers and sterile teeth at the top of the andro-column. Petals are contort to the right. 2.33. Side view of early anthers and teeth. Petals (scars show were there were removed) are opposite the teeth and are adnate to the androecium. Anthers appear to differentiate simultaneously. 2.34. Side view of partial androecium with terete teeth. Anthers are well formed, filaments are relatively short. The gynoecium lags behind the androecium in elongation. The gynoecium is beginning to differentiate into ovary (v), styles (sl), and early stigmas (sm). Individual styles are distinguishable all the way to the top of the ovary. 2.35. Capitate stigmas emerging above the sterile andro-teeth. The filaments are retrorse and diverge singly from the column. Note that some of the filaments on this immature column are in pairs. Nectarial trichomes (N) develop on the inner side of the sepals. Petal scars show adnation to androecium.

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Figs. 2.36 - 2.37. *Malvaviscus arboreus* var. *Drummondii*, pollen and young fruit. Bars = 200 μm in 2.36, = 2 mm in 2.37. 2.36. Nearly mature pollen grains (pg) in microsporangium. Pollen is spheroidal, polyporate, and echinate. 2.37. Cross-section of young fruit with five locular cavities, with one ovule in each. Note that there is no visible distinction between the tissue from the sterile and fertile carpel walls.
The surface of the mature ovary is circular and smooth; there are no indentations or lobing (Figs. 2.34, 2.37) to indicate the location of ovules to the interior. The mature fruit is a smooth, fleshy schizocarp or berry. The bractlets and sepals persist in the fruit.

**Pavonia strictiflora (= Goethea strictiflora)** -- **Organography** -- The plants are large shrubs with axillary flowers, borne on short lateral spurs with crowded internodes. The four (sometimes three) involucellar bracts are broadly ovate and brightly colored (reddish). The five-lobed calyx is also reddish and is concealed by the involucel. The reddish, five-merous corolla is subequal to or slightly exceeds the calyx in length. The androecial column bears 45 to 50 stamens and is exserted beyond the involucel. The gynoecium is terminated by ten exserted stigmas. Each locule contains only one seed. The mature fruit type is unknown (observations of collected material; Fryxell, 1999).

**Organ initiation and early development** -- Four bractlets initiate in helical order (Fig. 2.38). Stages are lacking for this species to show if a low ring develops before the bracts. The pre-sepal apex is four-angled due to appression of the bractlets (Fig. 2.39) and the apex is not as flat as in *M. arboreus*. A low ring appears around the periphery of the pre-sepal apex (Fig. 2.40). The pattern of sepal initiation appears to be helical (Figs. 2.40, 2.41). Even after the five sepal primordia are well formed, the flower is still four-sided. As in *M. arboreus*, the sepals in *P. strictiflora* are fused at the base from early ontogeny.

The pre-petal apex is slightly convex, and pentagonal in outline. A petal-stamen ring meristem forms. On this ring, petals and the first and second sets of common stamen primordia arise (Figs. 2.42, 2.43) in the way...
described for *M. arboreus*. Petal primordia, however, do not broaden and do not become blade-like as early in ontogeny (Figs. 2.43, 2.44). Also, there are more stamens (usually 45), so the common primordia persist longer and divide more times. The third and fourth sets of common stamen primordia are initiated centripetally to the first and second sets, respectively. Initiation of the third set slightly precedes initiation of the fourth set (Figs. 2.43, 2.44). A fifth set of stamen primordia initiates centrifugally to the first set (Fig. 2.44). This differs from *M. arboreus* in which the third set of stamen primordia is centrifugal. In *P. strictiflora*, initiation of this centrifugal set is delayed. The third and fourth sets of common stamen primordia radially broaden and bifurcate centripetally to form the sixth and seventh sets of stamen primordia (Fig. 2.45). The first and second sets of common stamen primordia then bifurcate in an oblique centrifugal direction to form the eighth and ninth sets of stamen primordia (Figs. 2.45, 2.46). Sometimes it appears as if a tenth set of primordia initiates centrifugally to the ninth set. Initiation within each set of five primordia is simultaneous. Much variation occurs in this model of stamen initiation in *P. strictiflora*. For instance, random lone primordia can arise at various locations on the ring meristem; sometimes not all the primordia in a set initiate; or extra divisions of common primordia may occur.

The inner surface of the ring becomes pentagonal in outline, but unlike *M. arboreus*, the sides of the pentagon alternate with the petals (Figs. 2.44, 2.48). Five sterile teeth primordia form to the interior of the young andro-column and alternate with the petals (Figs. 2.47, 2.48). As the column elongates upward, each of these teeth may fork one or two times so that there are many teeth of various sizes at the apex of the column (Fig. 2.54).
The first five carpel primordia initiate before initiation of the sixth and seventh stamen sets (Fig. 2.44). Unlike in *M. arboreus*, these carpels are opposite the petals (Fig. 2.44). Five more carpels initiate alternately to the first five (Fig. 2.48). Initiation within each set of five is simultaneous and both sets are within the same spatial whorl. All ten carpels develop a dimple on the lower interior surface (Fig. 2.49). All these dimples produce crevices, but they are more pronounced in the fertile (second set) carpels (Fig. 2.50). The sterile carpels are usually slightly taller than the fertile carpels (Figs. 2.49 - 2.53). As the carpel primordia enlarge, the crevices in the sterile carpels disappear; crevices in the fertile carpels become more defined (Figs. 2.51, 2.52). These early signs of locule formation occur at about the time anthers and filaments are differentiating. Unlike *M. arboreus*, in *P. strictiflora* the walls of the fertile carpels appear to merge with those of the sterile carpels to form the sides of the locular cavities (Fig. 2.52). In addition, both sets of carpels remain at the periphery of the column (Figs. 2.52, 2.53). As the styles differentiate, lobing occurs on the outside of the ovary, demarcating the position of the developing locules (Fig. 2.53). One ovule forms in each locule. The floral apical residuum persists (Fig. 2.51, 2.52) and is not incorporated into the carpel primordia.

**Midstage and mature reproductive characters** — The bractlets remain distinct and become larger and more showy than the perianth. The involucel does not spread in the mature flower; the bractlets form an open-top box-like structure with their adjacent margins meeting and flaring outward rather than overlapping. The basally fused sepals close over the top of the floral apex temporarily during subsequent organ initiation. At maturity, the sepals are fused about half of their length. Nectarial trichomes form on the inner surface
Figs. 2.38 - 2.41. *Pavonia strictiflora*, initiation of bractlets and sepals. Bractlets have been removed in Figs. 2.39 - 2.41. Bars = 100 μm. 2.38. Helically initiated bractlet primordia (order of initiation shown by numbers). 2.39. Four-sided pre-sepal apex with appression marks from the bractlets. 2.40. Shallow ring meristem with early sepal primordia. 2.41. Helical initiation of five sepal primordia on a four-sided apex (order of initiation shown by numbers), two oldest sepal primordia appear on sub-opposite sides of the apex. The pre-petal apex is convex.
Figs. 2.42 - 2.47. *Pavonia strictiflora*, petal and stamen primordia. Bractlets and sepals have been removed. Bars = 200 μm. 2.42. Petal primordia with first and second sets of common stamen primordia. 2.43. Initiation of the third and fourth sets of common stamen primordia centripetally to the first and second sets. 2.44. Further development of the third and fourth sets of common stamen primordia and initiation of the fifth set centrifugally. Petals are narrow (i.e. have not broadened). Slight mounding on the inner surface of the ring indicates the initiation of sterile teeth. 2.45. Bifurcation of common stamen primordia to yield sixth and seventh sets of stamen primordia. The first and second common stamen sets have broadened. 2.46. Eight and ninth sets of stamen primordia result from bifurcation of the first and second sets. 2.47. Differentiation of anthers and five sterile teeth.
Figs. 2.48 - 2.53. *Pavonia strictiflora*, development of the gynoeicum. Bars = 200 μm in 2.48 - 2.50, = 500 μm in 2.51 - 2.53. 2.48. The carpels are in a single spatial whorl. Members of the first set that formed are opposite the petals and alternate with the sterile teeth primordia. 2.49. Dimples form (at arrows) in both sterile and fertile carpels. The androecial column (Ad) has been removed. The fertile carpels (second set) are slightly shorter than the sterile carpels. 2.50. Crevices in the fertile carpels are more pronounced than in the sterile carpels. 2.51. Crevices in the fertile carpels have deepened; those in the sterile carpels have disappeared. The floral apical residuum persists. The androecial tube is forming with apical sterile teeth. 2.52. The walls of the fertile carpels are merging with those of the sterile carpels to form the locular cavities. 2.53. All ten young styles remain at the periphery of the column. Indentations/lobing of the ovary indicates the position of the five developing locules.
Figs. 2.54 - 2.57. *Pavonia strictiflora*, midstage and late development.

Bars = 1 mm in 2.54 - 2.56, = 200 μm in 2.57. **2.54.** Side view of young androecial column with several anthers removed to show paired filament divergence. The original five sterile teeth are forked, giving the appearance of more teeth. **2.55.** Longitudinal section of bud showing petal-stamen column adnation, sepal nectaries, and differentiation of organs. The bractlets have been removed. **2.56.** Oblique view of lower portion of stylar column and segmented ovary. External separations between individual styles shown with arrows. This aberrant ovary has six lobes. **2.57.** Dehiscing anther sac with mature pollen grains that are spheroidal, polyporate, and smooth.
of the sepals (Fig. 2.55). The petals are adnate to the androecial column (Fig. 2.55) and lack auricles.

Anther differentiation is nearly simultaneous among all stamens. The filaments elongate, diverging from the andro-column singly and in pairs (Fig. 2.54). Many sterile teeth (actually five multi-lobed teeth) terminate the column (Fig. 2.54). Selective elongation of the androecial column brings the level of filament attachment to the top fourth of the column at maturity; the filaments are only slightly retrorse and are radially displayed around the column. The anthers dehisce by longitudinal slits at the sutures between the two sporangia.

Initially, the gynoecium lags behind the androecium in elongation and differentiation (Figs. 2.51, 2.52, 2.54, 2.55). The separation between styles on the outer column surface is not quite complete to the top of the ovary (i.e. the styles are free distally but the individual styles become less distinct at their connate bases) (Fig. 2.56). In the mature flower, stigmas are emergent and capitate. The styles of the sterile carpels are equal to, or taller than, the styles of fertile carpels. Both the androecium and gynoecium are exserted beyond the contort corolla; the gynoecial column is about double the corolla in length. The styles separate at the upper third of the gynoecial column.

There is no twisting in the androecium or gynoecium. There may be slight zygomorphy in the gynoecium in that the terminal portion of the styles bend slightly upward; lack of material makes this inconclusive. The pollen is spheroidal, smooth (no spines), and polyporate (Fig. 2.57). The base of the ovary has five (rarely more) distinct lobes (Fig. 2.56) indicating the position of enclosed locules. Each locule contains one ovule.

**Pavonia bahamensis - Organography** – These shrubs have solitary flowers in the axils of leaves. The flowers are tubular in shape. The five to ten
green involucellar bracts are lanceolate. Five green sepals are subequal in length to the involucre. The corolla is pentamerous, tubular, and greenish yellow. The androecium consists of approximately 35 stamens and is exserted. The gynoecium is terminated by ten exserted stigmas. Fruits are schizocarps with one ovule per mericarp (observations of collected material; Fryxell, 1999).

Organ initiation and early development -- The involucel bractlets initiate in helical order on a low ring meristem on the floral apex (Fig. 2.58). The pre-sepal apex is slightly convex (Fig. 2.58). Next, a pronounced pre-sepal ring forms (Fig. 2.59). The ring is multi-sided in accordance with the number of bractlets (Fig. 2.59). Sepal initiation on the ring appears to be helical, with the first two sub-opposite (Figs. 2.59, 2.60). The five sepals are fused at the base from the time of early initiation (Fig. 2.60).

The pre-petal apex is slightly-convex and pentagonal in outline (Fig. 2.59). The steps from initiation of a petal-stamen ring to initiation of the second set of common stamen primordia proceed in the same way as described for *M. arboreus*. As in *P. strictiflora*, the third set of common stamen primordia initiates to the inside of the first set of common stamen primordia (Fig. 2.61). A fourth set of stamen primordia initiates centrifugally to the second set of common stamen primordia at about the same time that the first, second, and third sets of common stamen primordia are beginning to broaden in an oblique centripetal direction (Figs. 2.62, 2.63). These common stamen primordia bifurcate to form the fifth, sixth, and seventh sets of stamen primordia (Figs. 2.63, 2.64). Initiations within each of these seven sets of stamen primordia are simultaneous.

The space remaining on the inner surface of the ring meristem is opposite but off center with respect to the petals (Fig. 2.61). Critical stages for
initiation of the five sterile teeth are lacking for this taxon. In later stages, the position of the teeth with respect to the petals is unclear, but appears to be opposite and off-center (Figs. 2.65, 2.68).

Some sterile teeth become two-lobed at the apex (Fig. 2.65) and some may fold longitudinally inward slightly (Fig. 2.65), forming a suture-like line of cells that extends from near the apex of the tooth to the base of the inner surface of the androecial column (Fig. 2.67). This feature makes it difficult to tell orientation of the first and second carpel sets when using suture lines between sterile teeth as an orienting feature.

Carpel initiation occurs after initiation of the fourth set of stamen primordia. The first five carpel primordia initiate (Fig 2.66) alternate with the sterile teeth, i.e. at the corners of the remaining pentagonally-shaped apex and therefore, alternate with the petals, but off-center with respect to each. As with the previously mentioned taxa, the second set of five carpel primordia initiates alternately to the first set of carpel primordia, and both sets are within the same spatial whorl (Fig. 2.66). Initiation within each set of five carpel primordia is simultaneous.

Only the second, smaller set of carpels invaginates (Fig. 2.67). This occurs at the same time that the stamen primordia are differentiating into filaments and anthers. The invaginations in the fertile carpels deepen and the upper part of the primordia arch inward (Fig. 2.68). Unlike in M. arboreus, the sides of the fertile carpels in this taxon appear to form part of the walls of the locules (Fig. 2.68). The taller sterile carpels grow towards the center of the column, whereas the shorter fertile carpels remain more towards the periphery (Fig. 2.69). One ovule forms in each fertile carpel (Fig. 2.69). As in the former
taxa, the floral apical residuum persists and is not incorporated into the gynoecium.

**Midstage and mature reproductive characters** -- The involucellar bracts remain distinct and immediately subtend the calyx. The mature calyx is tubular, with sepals fused more than four-fifths of their length. Nectarial trichomes are found on the inner side of the sepal bases. Petals are adnate to the base of the androecial column and lack auricles. The petals are about double the length of the calyx at maturity. The corolla is tubular in shape.

Anther differentiation is nearly simultaneous (Fig. 2.65). The median groove between the two microsporangial regions of the anthers is discernible after the ten carpels have been initiated. The two microsporangia composing each anther are very distinct (Figs. 2.65, 2.70) before the filaments begin to elongate. The filaments diverge singly, often roughly spaced in three whorls at the upper third of the androecial column. The filaments are not retrorse. An unusual feature of this species is that the filaments bend to present the anthers on one side of the androecial column, so that all anthers are on the upper side of the androecial column in the horizontally positioned flowers. Anthers dehisce by longitudinal slits at the sutures between the two sporangia, opening each sporangium where they were attached to each other. Early in development, the sterile teeth often become two-lobed (Figs. 2.65, 2.68). At first not much enlargement occurs in the lobes of the sterile teeth, and fusion causes the individual teeth to become less distinct at the apex, so that as the androecial column enlarges, it is crowned by a tube with many small apical projections (Fig. 2.70). At maturity, the teeth are narrowly triangular in shape and of various sizes. The number of mature teeth usually appears to be ten.
Figs. 2.58 - 2.65. *Pavonia bahamensis*, selected stages of initiation of bractlets, sepals, petals, and stamens. Bars = 200 μm. 2.58. Helical initiation of bractlets on two floral apices. The younger floral apex has a low rim on which the bractlets are starting to initiate. The possible sequence in initiation of the bractlets is shown with numbers on the older floral apex. The pre-sepal apices are slightly convex. 2.59. Pre-sepal ring at arrow. The outside of this pre-sepal ring is eight-sided in accordance with the number of bractlets. The inside of the pre-sepal ring and remaining floral apex are pentagonal in outline and the floral apex is slightly convex. Order of sepal initiation is difficult to determine; the first ones in each set (labeled 1) are presumably the five on the area of the ring with higher and broader mounding. 2.60. Sepal primordia. The two largest primordia (marked with S) appear to be on sub-opposite sides of the flower. The order of the three unnumbered sepals can not be determined from this micrograph. Note early fusion at the bases of the sepals to form a connate calyx. 2.61. Common petal-stamen ring with petal primordia and the first, second, and third sets of common stamen primordia. Remaining meristematic space on the interior of the ring is opposite but off-center with respect to the petals. 2.62. Initiation of the fourth set of stamen primordia and oblique centripetal broadening of the first, second, and third sets of common stamen primordia. 2.63. Bifurcation of the first, second, and third sets of common stamen primordia to yield the fifth, sixth, and seventh sets of stamen primordia, respectively. 2.64. Thirty-five stamen primordia on petal-stamen ring meristem. 2.65. The five sterile teeth are apically bilobate and are positioned opposite and off-center to the petals.
Figs. 2.66 - 2.71. *Pavonia bahamensis*, selected stages of carpel initiation and midstage and late floral development. Bars = 200 μm in 2.66 - 2.69, = 2 mm in 2.70, = 100 μm in 2.71. 2.66. The first five carpel primordia (two are numbered 1) initiate in the corners of the remaining floral meristem, i.e. alternate and off-center with the petals. The second set of five carpel primordia (one is numbered 2) are alternate with the first set and in the same spatial whorl. 2.67. Gynoecial whorl with adaxial dimples in the slightly smaller second set of carpel primordia. Suture between sterile teeth at arrow A; suture caused by folding of sterile teeth at arrow B. Distinction between suture types was determined by a more encompassing view. 2.68. Androecium and carpel primordia. The androecial tube is elongated with apical sterile teeth. Crevices (at arrow) develop in the fertile carpels. The sides of the fertile carpels form part of the crevice walls and the tops of the fertile carpels grow inward towards the center of the column. Identification of the first-formed sterile carpel primordia is determined by reference to the two-lobed sterile tooth. 2.69. Gynoecium. Sterile carpels are taller and more to the center of the column than the fertile carpels. One ovule is present in the locule of each fertile carpel. 2.70. Late stage (but not quite mature stage) of floral development with sterile teeth formed into a tube with small apical projections. Capitate stigmas are exserted beyond the androecial tube. 2.71. Pollen grain prior to anthesis. Pollen is spheroidal, echinate, and polyporate.

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Initially, the gynoecium lags behind the androecium in elongation and differentiation (Fig. 2.68). The stigmas begin to differentiate before they surpass in length the sterile teeth of the androecial column. All ten styles form exserted capitate stigmas (Fig. 2.70). At maturity, the gynoecium is nearly a third longer than the corolla. The styles separate only at the very tip of the gynoecial column (about the upper tenth to fifteenth).

There is no twisting of the androecial or gynoecial column in the mature flower. The androecium is zygomorphic in that the anthers are displayed on one side of the column. The doubling of the stamen teeth in *P. bahamensis* produces an atypical number of teeth (about ten); members of this tribe usually have five. The pollen grains are spheroidal, echinate (the spines with rounded tips), and polyporate (Fig. 2.71).

The fruit is five-locular with axile placentation and one ovule per locule. The surface of the ovary appears relatively smooth with only slight lobing evident. Only immature fruits were available for study, so a description of the mature fruit was provided by Fryxell (1999). The fruit is a glabrous, subglobose (slightly wider than tall), schizocarp. Each mericarp has a broad lateral wing.

**Pavonia spinifex** — **Organography** — The plants are shrubs with solitary flowers in the leaf axils. The involucel consist of five to ten ligulate bractlets. The calyx is five-lobed, and equal or slightly subequal in length to the involucel. The five-merous corolla is yellow. Approximately 40 stamens and five sterile teeth form the androecial column. The gynoecium is terminated by ten styles. The gynoecium and androecium are equal in length or slightly exserted beyond the corolla. The fruit is a spiny schizocarp. Each locule contains one seed (observations of collected material; Fryxell, 1999).
Organ initiation and early development -- The involucel bractlets initiate in helical order on a low ring on the floral apex (Figs. 2.72, 2.73) and the pre-sepal apex is slightly convex (Fig. 2.73). The pre-sepal ring meristem is low and multi-sided in accordance with the number of bractlets (Fig. 2.74). Sepal initiation appears to be helical with the first two sub-opposite (Fig. 2.74). The five sepals are fused at the base.

Initiation of the petal-stamen ring meristem, initiation of the petal primordia, and initiation of the first and second sets of common stamen primordia proceed as in *M. arboreus* (Fig. 2.75). Approximately 40 stamen primordia form. The complete pattern of initiation is not known, but the last stages involve bifurcation of 15 common stamen primordia (three sets of five primordia) in an oblique centripetal direction (Fig. 2.76). Based on equal primordial sizes, initiation within each set of five stamen primordia is believed to be simultaneous (Fig. 2.76). Five sterile teeth form at the apex of the androecial column. As in *P. bahamensis*, the teeth are opposite to and off-center with the petals.

Early stages of carpel initiation are lacking for *P. spinifex*. At later stages, as in previously described taxa, there are ten carpel primordia present in a single spatial whorl; with five of the carpels larger than five alternates. Therefore, it is reasonable to assume that carpels in *P. spinifex* initiate the same way as described for previous taxa; with two sets of five carpel primordia initiating within a single whorl and simultaneous initiation within each set of five carpel primordia. Only the five smaller carpels form crevices (which precede locule formation), but there is evidence of slight dimples forming in the larger carpels (Fig. 2.77). The sides of both the fertile and sterile carpels form the radial walls of the locules (Fig. 2.77). The early inward growth of the
bases of the sterile carpels is very pronounced in this species (Fig. 2.77). As apical elongation of the stylar region of the carpels occurs, the taller sterile carpel tips grow inward towards the center of the column. The fertile carpel tips are shorter and remain towards the periphery of the column (Fig. 2.78). The smaller fertile carpels alternate with the androecial teeth (Fig. 2.78). The floral apical residuum persists.

Midstage and mature reproductive characters -- The bractlets of the involucel remain separated from each other and immediately subtend the calyx. At maturity, the sepals are fused only a fourth to a third of their length. Numerous nectarial trichomes form at the base of the inner side of the sepals (Fig. 2.81). The petals are adnate to the base of the androecium and they lack auricles. The mature corolla spreads and is about double the length of the calyx.

Some stages of stamen differentiation and carpel differentiation are lacking in my material. At maturity, the androecial column is equal to or is only slightly exserted beyond the corolla. The filaments diverge radially from the upper third to fifth of the androecial column. The filaments may diverge singly or in pairs (Fig. 2.79) and are not retrorse. The anthers dehisce by longitudinal slits as in the previously described taxa. The five sterile teeth at the top of the column are distinct.

In the gynoecium, all ten carpels form emergent, capitate stigmas (Fig. 2.79). The gynoecium is only slightly longer than the corolla. As the ovary develops, five segments (which will become mericarps) are visible on the outside (Fig. 2.80). One ovule forms in each locule (Fig. 2.81) and placentation is axile. Each of these mericarps develops basal lobes at their margins and an apical ridge in the center (Fig. 2.81). Later, in the mericarps of
Figs. 2.72 - 2.78. *Pavonia spinifex*, selected stages of early floral development. Bars = 200 μm. 2.72. Floral apex in axil of leaf and accompanying stipules. A bractlet primordium has initiated on a low ring meristem. 2.73. Helical initiation of bractlets shown with numbers indicating order of initiation. The pre-sepal apex is slightly convex. 2.74. Pre-sepal ring meristem with sepal primordia. The two older primordia (S) appear to be sub-opposite. 2.75. Common petal-stamen ring with petal primordia and first (1) and second (2) sets of common stamen primordia (one primordium from each set of five is labeled). 2.76. Late stage of stamen initiation with bifurcation of 15 common stamen primordia (three sets of five). In this case, numbers represent sets of stamens and do not necessarily reflect the order of initiation. (Only one sectorial region has been labeled, i.e. one primordium from each set.) Initiation within each set of five primordia is simultaneous. The petal has broadened and produced a blade. 2.77. Five fertile carpel primordia with deep crevices and five alternate sterile carpel primordia with only slight dimples. Note the inward growth of the bases of the sterile carpels. 2.78. Gynoecium with elongation of stylar regions of the carpels. The fertile carpels are shorter and more to the periphery of the column. Fertile carpels are alternate with the androecial teeth. Androecial column has elongated, raising the teeth to the summit.

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Figs. 2.79 - 2.82. *Pavonia spinifex*, selected stages of midstage and late floral development. Bars = 500 μm in 2.79 - 2.81, = 100 μm in 2.82.

2.79. Midstage development of androecial and gynoeccial columns. Scars (at arrows) show that most filaments diverge in pairs. Five apical teeth are apparent at the top of the androecial column. The ten stigmas are capitate.

2.80. Young gynoeccial base with stylar column removed. Five segments (which will become mericarps) are apparent from the outside surface.

2.81. Gynoeccial base with stylar column removed. One ovule is shown in its locule. Basal lobes (arrows D) develop on each side of the mericarps and an apical ridge develops in the center (E).

2.82. Pollen grain that is spherical, echinate, and polyporate.
a mature schizocarp, the basal lobes form two lateral spines and the apical ridge forms an erect central spine. The spines are retrorsely barbed. The fruit shape is subglobose (excluding spines) and the surface texture is rugose. The calyx and involucel persist in the fruit.

The symmetry of the flowers is actinomorphic, and no twisting occurs in the androecia or gynoecia. The pollen grains are spherical, echinate (with pointed spines), and polyporate (Fig. 2.82).

_Malachra capitata_ -- Organography -- The plants are erect perennial herbs. Inflorescences are several-flowered capitula on mostly axillary peduncles. The two or more specialized floral bracts that subtend each capitulum are sessile, broadly ovate, cordate, and conduplicate. The bracts have whitish backgrounds (intercostal areas) with green veins and are larger and more showy than the flowers they subtend. The involucel is absent. The calyx is green with white intercostal areas and is five-lobed. The corolla is five-merous and yellow or orange in color. The staminal tube is included (shorter than the petals), five-toothed, and bears 10 - 15 (15 - 30 according to Correll and Johnston, 1979) stamens along the middle and upper portion of the column. The gynoecial column is terminated by ten styles and stigmas. The five mericarps of each schizocarpous fruit are brownish in color and smooth with reticulate veins. Each locule contains one seed (observations of collected material; Correll and Johnston, 1979; Fryxell, 1988).

Organ initiation and early development -- Flowers and subtending floral bracts on the capitulum initiate in an inwardly spiral clockwise (Figs. 2.83 - 2.85) or counterclockwise pattern. Thus, on a single head, the flowers and floral bracts are of various sizes during development (Figs. 2.83 - 2.85). In the early formation of the inflorescence, one floral bract initiates prior to initiation
of each floral apex (Fig. 2.83). The floral bracts initiate adjacent to the floral apices; not on the apices as do involucellar bracts. The floral bracts initiate as single mounds (Fig. 2.83, examples B4, B5); but as they enlarge, small lobes develop on the lateral flanks of each (Fig. 2.83, examples B1 - B3). The floral bracts are always to the periphery of the capitulum and thus appear, as a group, to subtend the entire inflorescence (Figs. 2.83 - 2.85). The capitula in this study never exceeded six flowers; thus all the floral bracts could easily be arranged around the perimeter of the head. A point for further investigation is whether more numerous-flowered capitula develop. If so, what is the fate of the floral bracts: do they occur in the center of the head, are they suppressed in growth, or do the bracts cease to initiate in later-formed flowers?

Involucellar bracts are lacking on the floral apex (Figs. 2.83, 2.86). On the floral apex, sepals initiate in a helical pattern with the first two sub-opposite (Fig. 2.86). The first two sepals are in a plane that is perpendicular to the median sagittal plane that bisects the flower and the subtending bract. It appears as if the sepals initiate on a low ring (Fig. 2.86). The sepals are fused at the base and as organ development begins, they equalize in size.

The pre-petal apex is pentagonal in outline and slightly convex (Fig. 2.86). On a low ring meristem, five common petal-stamen mounds (sectorial regions) form simultaneously (Fig. 2.87). As in *M. arboreus*, the mounds alternate with the sepals and subdivide into five petal primordia and five common stamen primordia (Figs. 2.87, 2.88). In *M. capitata*, however, the petal primordia alternate with the sepals, and the common stamen primordia are opposite and slightly off-center to the sepals, i.e. the common stamen primordia are mostly alternate to the petals rather than on the same radius as them (Figs. 2.88, 2.89). Unlike in *M. arboreus*, a second set of smaller
common stamen primordia do not form laterally to the first set. Instead, the first set of common stamen primordia enlarge into five very prominent mounds on the ring (Fig. 2.89), then broaden in an oblique direction that is away from the center of the associated petal primordia (Fig. 2.90) rather than toward them. Each common stamen primordium of the first set bifurcates to form two equal or nearly equal stamen primordia (Figs. 2.85, flowers 5 and 6; 2.91; 2.92). The two stamen primordia that result from each of these bifurcations are generally opposite different petals (Figs. 2.91-2.93). This is in contrast to M. arboreus, in which the proliferation of stamens from common stamen primordia form discrete groups that are in line with their associated petals (Figs. 2.13 - 2.15). Initiation of the five petal primordia (Fig. 2.88) and within each set of five stamen primordia (Figs. 2.89 - 2.91) is simultaneous.

The majority of M. capitata flowers examined in this study have ten stamens. Exceptions with 11 - 15 stamens were seen, but only as midstage floral buds; it is unclear where and how the additional stamens initiate. In the midstage buds with higher staminal merosity, the additional stamens are located towards the outer portion of the androecial column (Fig. 2.94).

The remaining inner portion of the androecial ring meristem expands inwardly, forming a rim that arches slightly over the remaining floral apex (Figs. 2.92, 2.94). The five sterile teeth develop concurrently with anther differentiation and the teeth appear to be opposite the petals (Fig. 2.98).

Carpel initiation begins at the time the first set of common stamen primordia is broadening (Fig. 2.95). The first five carpels initiate simultaneously and alternate with the petals, opposite the common stamen primordia (Fig. 2.95). A second set of five carpels initiates alternately to the first set in the same spatial whorl (Fig. 2.96). Initiation within this second set of
carpels is also simultaneous. Only the second set of carpels (opposite the petals) invaginate and form crevices (Fig. 2.96); this occurs after stamen primordia have begun differentiating into anthers and filaments. As in *M. arboreus*, the sterile carpels appear to form the sides of the locular cavities (Fig. 2.97). One ovule develops in each locular cavity before stylar elongation occurs (Fig. 2.97). As styles elongate, they all appear to be approximately equal in height and equidistant from the center of the column. As in the previously described taxa, apical residuum remains in the center of the young gynoecium (Figs. 2.96, 2.97).

**Midstage and mature reproductive characters** -- The sepals temporarily form a protective dome over the developing bud. At maturity, the calyx is deeply lobed (the sepals are fused a fourth to a third their length). Nectarial trichomes form at the base of the inner side of the sepals. The petals are attached to the base of the androecium (Figs. 2.98, 2.99) and are not auriculate. The mature petals exceed the calyx length by about a fifth to nearly half.

Anther differentiation appears nearly simultaneous in the androecium. The median grooves between microsporangial regions of each anther are discernible after initiation of the first set of carpel primordia. Each anther has developed two distinct microsporangia before invagination of the second carpel set begins and before elongation of the filaments. The filaments diverge singly or in pairs from the androecial column (Fig. 2.98). At maturity, the filaments diverge along most of the column, lacking only in the lower 1/5 to 2/5 on the column. They are not retrorse and are radially displayed around the column. As in the previously described taxa, the anthers dehisce by longitudinal slits at the sutures between the two sporangia. At first,
Figs. 2.83 - 2.88. *Malachra capitata*, inflorescence development and initiation of sepal, petal, and common stamen primordia. Bars = 200 μm in 2.83 - 2.85, = 100 μm in 2.86 - 2.88. **2.83.** Young capitulum. The youngest flowers are centrally located on the head. Floral apices (A) are numbered beginning with 1 as the first-initiated. The older floral bracts (B1 - B3) have smaller lobes on their lateral flanks (arrows show which lobes are associated with each bract). **2.84.** Partial capitulum. Younger flowers are towards the center and the floral bracts are all towards the perimeter of the head. Flowers are numbered in order of initiation. Flower 2 has been removed at the bottom of the micrograph. **2.85.** Capitulum that shows the centripetal, spiral pattern of floral initiation (order of floral initiation shown with numbers). All floral bracts, which have been removed, were presented to the outside of the head. **2.86.** Floral bud with sepal primordia. The two older (larger) sepals are labeled (S). It appears as if the sepals are on a low ring meristem. **2.87.** Common petal-stamen ring meristem with five common petal-stamen mounds. The mounds alternate with the sepals. **2.88.** Five petal primordia (alternate with the sepals) and five common stamen primordia (opposite and slightly off-center with the sepals).
Figs. 2.89 - 2.94. *Malachra capitata*, stamen initiation. Bars = 200 μm.  
2.89. Flower with five enlarged common stamen primordia. 2.90. The five common stamen primordia have broadened in an oblique direction. 2.91. Ten stamen primordia resulting from bifurcation of the original five common stamen primordia. Numbering of the stamen sets is somewhat arbitrary in this case since the bifurcation has produced equal or nearly equal-sized primordia (central primordia appear slightly larger in some micrographs). 2.92. Ten stamen primordia are present. Note that the two stamen primordia that resulted from bifurcation of each of the original common stamen primordia are aligned in front of different petals. The remaining ring meristem forms a rim around the remaining floral apex. 2.93. Flower with ten stamen primordia. One pair of stamens that resulted from the bifurcation of a common stamen primordia is labeled 1 and 2. Note that each member of the pair is generally in line with a different petal. 2.94. Midstage floral bud with eleven anthers. Extra anther indicated with (*). The tissue that remains from the inner portion of the androecial ring has elongated with the androecial column and is arching over the remaining floral apex. On this rim a sterile tooth lobe is barely discernible.
Figs. 2.95 - 2.100. *Malachra capitata*, selected stages of carpel initiation and midstage floral development. Bars = 100 μm in 2.95 - 2.97, = 1 mm in 2.98 and 2.99. 2.95. First five carpel primordia (sterile carpels) are alternate with the petals and opposite the common stamen primordia. 2.96. Ten carpel primordia in a single spatial whorl. The fertile carpels are opposite the petals, thus are the second-formed set. Because of the reduction in size and merosity of the androecial column, direct alignment of the carpels to the petals (rather than the sterile teeth) was possible for this taxon. 2.97. Gynoecial whorl with upper portion of two carpels removed. Only the invaginated member of the second set of carpels forms an ovule. 2.98. Young androecial and gynoecial columns. Filaments diverge singly from the androecial column (at arrows). The sterile teeth are broad lobes. Ten capitate stigmas terminate the gynoecium. Petals are adnate to the androecial column. Notice that the androecial tube bulges around the ovary so that from this view the petals appear to be attached to the edge of an androecial shelf. 2.99. Gynoecial column in partial androecial column. Note that the androecial column curves around the ovary. The styles are all the same length. The base of the stylar column is fused and individual styles are indistinguishable; styles separate from the column only at the apex. The stigmas are capitate. The ovary base is five-lobed, rugose, and bears trichomes. 2.100. Pollen grains are spheroidal, echinate, and polyporate.
the sterile teeth are broadly rounded, thick lobes (Fig. 2.98). As the apical

teeth mature, they become rounded in shape.

Initially, the gynoecium lags behind the androecium in development and
elongation. As the gynoecial column matures, the styles fuse at the base and
are only distinguishable in the upper portion of the column (Fig. 2.99). The
stigmas begin to differentiate before they surpass in length the sterile teeth of
the androecial column. The ten styles are equal in height and exserted
beyond the androecial column (Figs. 2.98, 2.99). The stigmas are capitate
(Figs. 2.98, 2.99). The gynoecial column is included, its length approximately
1/6 shorter than the length of the petals. The styles separate from the column
only near the apex (upper fifth).

There is no twisting in the gynoecial or androecial columns. Floral
symmetry is actinomorphic. The pollen grains are spheroidal, echinate (the
spines long and blunt-tipped), and polyporate (Fig. 2.100). The young ovary is
distinctly five lobed, slightly rugose, and has many trichomes (Fig. 2.99). The
fruit is five-locular. One ovule develops in each locule and placentation is
axile. The sepals persist around the schizocarp.

**Urena lobata** -- *Organography* -- The plants are subshrubs with one or
a few flowers on short pedicels or subsessile in the leaf axils. The involucel
consists of five green bractlet lobes that are subequal to equal in length to the
calyx (sometimes they slightly exceed the calyx). Bractlets alternate with the
five green sepal lobes. The pink or lavender corolla is five-merous and
diverges distally. The androecial column is included and bears 15 - 30
subsessile anthers and five sterile teeth. The gynoecium is terminated by ten
styles and stigmas. Each oblate (subglobose) schizocarpic fruit consist of five
mericarps and is covered with numerous spines. The fruit separates into five
indehiscent segments with one seed in each (observations of collected material; Godfrey and Wooten, 1981; Fryxell, 1988).

**Organ initiation and early development** — The floral apices initiate in the axils of leaf primordia (Fig. 2.102). The five involucellar bracts initiate in helical order (Figs. 2.101, 2.102). The bractlets do not appear to form on a ring meristem (Fig. 2.101). Fusion at the base of the bractlets is not very pronounced until some time after all the sepals have initiated (Figs. 2.104 - 2.106). The pre-sepal apex is slightly convex (Fig. 2.102). There is no clearly defined ring meristem prior to or at the time of sepal initiation. The only indication that a ring meristem might be involved in sepal initiation is that the margin of the pre-sepal apex is slightly raised and the center is slightly concave (Fig. 2.103). Initiation of the five sepals appears to be simultaneous (Fig. 2.103). Fusion at the base of the sepals is not evident (Figs. 2.110 - 2.115) until anthers begin to differentiate by apically expanding and forming median grooves between the microsporangial regions.

The pre-petal apex is slightly convex and pentagonal in outline (Fig. 2.104). A ring meristem forms with five common petal-stamen mounds (Fig. 2.105). These common petal-stamen mounds form simultaneously and alternate with the sepals (Fig. 2.105). As in *M. arboreus*, these common petal-stamen mounds (sectorial regions) subdivide into five petal primordia and five common stamen primordia (Figs. 2.106, 2.107). Petal initiation is simultaneous (Figs. 2.106, 2.107). Initially, the petal primordia are alternate and slightly off-center with the sepals, and the common stamen primordia are opposite to the sepals but off-center (Figs. 2.106, 2.107). As the petals and common stamen primordia broaden laterally, however, both sets of organs become realigned alternate with the sepals (Fig. 2.108). The common stamen
primordia become aligned in radii that are almost opposite to the broadening petal primordia (Fig. 2.108).

Unlike _M. arboreus_ (in which the initiation of a lateral second set of stamen primordia precedes initiation of a third centrifugal set), in _U. lobata_, the lateral and centrifugal sets of common stamen primordia usually form concurrently (Figs. 2.108, 2.109). In some floral apices, stamen initiation stops with these 15 (three sets of five) primordia. In most, however, each primordium of the first set of common stamen primordia broadens in an oblique centripetal direction (Fig. 2.109), then bifurcates to yield a fourth set of stamen primordia (Fig. 2.110). Proliferation can continue with oblique centrifugal bifurcations of part or all of the second and third sets of common stamen primordia (Fig. 2.111). Within each set of five stamen primordia, initiation is simultaneous (Figs. 2.107-2.111). The inner surface of the androecial ring meristem initiates sterile teeth after the three sets of common stamen primordia have initiated (Fig. 2.110). Unlike in _M. arboreus_, the sterile teeth in _U. lobata_ are alternate with the petals.

Carpel initiation (Fig. 2.113) occurs after the three sets of common stamen primordia have initiated. It appears that the first five carpels initiate in the corners of the pentagonally shaped pre-carpel apex (Fig. 2.113). This means that the first five carpels in this taxon alternate with the sterile teeth and therefore, are opposite the petals. The second set of five carpel primordia alternate with the first set and are in the same spatial whorl (Figs. 2.113, 2.114). Initiation within each set of five carpels is simultaneous. All ten carpels form dimples (Fig. 2.114), that become crevices (Figs. 2.115-2.117). The carpel primordia opposite the petals (the first-formed set of carpels) become broad, with wide crevices (Figs. 2.115 - 2.117). The carpel primordia
of the second set (those that are alternate to the petals and opposite the
teeth), do not broaden and the crevices remain very narrow; the sides of the
adjacent carpel primordia appear to be pressing the sterile crevices closed
(Fig. 2.116). The sides of the locular cavities appear to be formed primarily by
the sides of the fertile carpels, but the sterile carpels are also involved (Fig.
2.116). The tips of the carpel primordia elongate (Fig. 2.118). The interior
bases and the apices of both sets of carpels remain equidistant from the
center of the column (Figs. 2.117 - 2.118). The styles of both sets of carpels
are approximately equal in height (Figs. 2.118 - 2.119). The external bases of
the carpels are fused from early in development (Figs. 2.117 - 2.119). The
bases of the fertile carpels broaden so that the young ovary becomes five-
lobed (Fig. 2.119). One ovule forms in each of the five locules (Fig. 2.121)
before the styles elongate. As in the previous taxa, an apical residuum
remains in the center of the floral apex and is not initially incorporated into the
gynoecium.

Midstage and mature reproductive characters -- The bractlets are
basally fused for about a fifth of their length, and immediately subtend the
calyx. The sepals temporarily close over the developing floral apex to form a
protective dome. Very little basal fusion of the sepals is evident until late in
development, when they are connate for about a fifth of their length. The
lobes of the calyx (which alternate with the involucellar lobes) equal or slightly
exceed the length of the involucel. Numerous nectarial trichomes form at the
base of the inner side of the sepals. The petals are adnate to the base of the
androecial column (Figs. 2.113, 2.119, 2.120). The mature corolla is double
to triple the length of the calyx. The distinct (unfused) petals spread distally
and lack auricles.
After all the carpel primordia have initiated, the anthers begin to differentiate, i.e. distal portions enlarge (Fig. 2.114) and indentations occur between the microsporangial regions (Fig. 2.115). The more recently formed sets of stamen primordia lag behind the older sets in anther differentiation (Figs 2.112, 2.115). The filaments become distinct from the anther regions of the stamens (Figs. 2.119, 2.120), but little elongation occurs so that in the mature androecial column, the anther are nearly sessile (Fig. 2.123). The filaments diverge singly or in pairs (Fig. 2.123). The androecial column is shorter than the corolla, and the anthers are radially displayed on the upper half of the column (Fig. 2.123). As described for previous taxa, the anthers dehisce by longitudinal slits along the sutures between two sporangia (Fig. 2.123). The five sterile teeth at the apex of the androecium are barely definable protuberances and are alternate in relation to the petals (Figs. 2.120, 2.123).

The styles of the gynoecium fuse so that they are indistinct until they separate at the apex (approximately upper tenth of the column) (Figs. 2.120, 2.122). No difference in height is discernible between the styles (and stigmas) of the fertile and sterile carpels. The stigmas in a flower of this taxon do not differentiate until after the styles have surpassed the androecial column in height. All ten carpels form capitate stigmas that are slightly exserted beyond the androecium (Fig. 2.123). The gynoecial column is about a third shorter than the corolla. The ovary base becomes distinctly five-lobed, with axile placentation and one ovule in each locule (Fig. 2.121). At maturity, the ovary is covered with trichomes and multi-lobed spinal protuberances (Fig. 2.122).

No twisting occurs in the androecial or gynoecial columns. The flower symmetry is actinomorphic. The pollen grains are spheroidal, echinate (the
Figs. 2.101 - 2.106. *Urena lobata*, initiation of bractlets, sepals, and petal-stamen ring meristem. Bars = 100 μm. 2.101. Floral apex with four (of five) bractlet primordia initiated. The pre-sepal apex is slightly convex. 2.102. Possible order of bractlet initiation illustrated with numbers, beginning with 1 as the first-initiated. The floral apex initiates in the axil of the leaf, with its two stipules. Bractlets do not appear to be basally fused. 2.103. Simultaneous initiation of sepals. The pre-petal apex is slightly concave. Bractlet scars indicate that they are still distinct. 2.104. Sepals equal in size and showing little basal fusion. The pre-petal apex is convex and pentagonal in outline. 2.105. Common petal-stamen ring meristem with five common petal-stamen mounds. The remaining floral apex is recessed at the center. The bractlets are slightly basally fused. The sepals are still relatively distinct. 2.106. Pronounced petal-stamen ring meristem around a concave meristem. Simultaneous initiation of five petal primordia and five common stamen primordia.
Figs. 2.107 - 2.112. *Urena lobata*, initiation of the corolla and androecium. Bars = 200 μm. 2.107. Common petal-stamen ring meristem. Five petal primordia alternate and slightly off-center with the sepals. The five common stamen mounds are opposite and off-center the sepals (i.e. each common stamen mound is opposite half of a sepal blade). 2.108. Initiation of the lateral (2) and centrifugal (3) sets of common stamen primordia. Numbering in this case is arbitrary since both sets appear to form concurrently. 2.109. The three sets of common stamen primordia (one from each set is labeled 1, 2, and 3) are now opposite to the broadened petal blade. Organs of the sectoral group (1, 2, 3, and P) are positioned alternate to the sepals. The first set of common stamen primordia have broadened in an oblique centripetal direction. 2.110. Bifurcation of first set of common stamen primordia to yield a fourth set of stamen primordia. Sterile teeth are initiating on the inner side of the androecial ring meristem. The teeth are alternate with the petals. 2.111. Bifurcation of the second and third sets of common stamen primordia to form (respectively) fifth and sixth sets of stamen primordia. 2.112. Anther differentiation is simultaneous within each set of five primordia, but not between sets throughout the androecial column. The earlier formed stamen primordia at the apex of the column are more differentiated (i.e. have more enlarged distal portions with more discernible indentations between microsporangial regions) than the peripheral primordia.
Figs. 2.113 - 2.118. *Urena lobata*, gynoecial initiation and early development. Bars = 200 μm. 2.113. Ten carpel primordia in one spatial whorl. The first-formed set (1) of five carpel primordia are in the corners of the pentagonal apex (i.e. opposite the petals). The second set (2) of five carpel primordia are initiating alternate with the first (i.e. alternate with the petals). 2.114. All ten carpels form dimples. Stamen are still proliferating. 2.115. Crevices form in both the sterile and fertile carpels. The carpels opposite the petal scars (fertile carpels) are broader with wider crevices than the sterile carpels. Anthers have begun to differentiate. 2.116. Gynoecial whorl with broad fertile carpels and narrow sterile carpels. The crevices in the sterile carpels are pressed closed. 2.117. Polar view of gynoecial whorl. Scars of the androecium, petals, sepals, and bractlets show the relative positions of the fertile and sterile carpels. 2.118. Young gynoecial column. Styles are all equidistant from the center of the column. All the carpels are approximately the same height. The external bases of the carpels are fused and the fertile carpels (alternate with the teeth) have broadened to make the ovary base five-lobed.
Figs. 2.119 - 2.126. *Urena lobata*, mid and late stage floral development. Bars = 100 μm in 2.119 and 2.124, = 500 μm in 2.120 - 2.123 and 2.126, = 2 mm in 2.125. 2.119. Partial androecial column and gynoecium. The ovary base is five-lobed. Sterile and fertile carpel styles are approximately equal in height. Fertile carpels alternate with the androecial teeth. 2.120. Androecial column with petals and some stamens removed. The stigmas have broadened and the appendages of the stigmatic surface have initiated. The sterile teeth are alternate with the petal scars. Some staminal filaments diverge singly, some in pairs. Petals are adnate to the androecium. 2.121. Five-locular ovary with one ovule in each locule. 2.122. Ovary at the time of floral anthesis. The styles are fused into a column. The ovary is covered with trichomes and spinal protuberances. 2.123. Upper portion of mature androecium and gynoecium. The anthers are nearly sessile, radially arranged around the column, and diverge singly or in pairs. Anther dehiscence is by longitudinal slits. Capitate stigmas terminate the styles. 2.124. Pollen grain in dehisced anther. The pollen is spheroidal, echinate, and polyporate. 2.125. Deeply five-lobed schizocarp with persistent bractlets and sepals. The surface of the mericarp bears numerous trichomes and retrorsely barbed spines. 2.126. Nearly mature spines and trichomes on surface of fruit.
spines long with blunt tips), and polyporate (Figs. 2.123, 2.124). The fruit is a subglobose schizocarp with five prominent lobes (Figs. 2.125). In addition to numerous trichomes, each mericarp is covered with spines bearing several retrorse apical barbs (Figs. 2.125, 2.126). The bractlets and sepals persist in the fruit (Fig. 2.125).

**DISCUSSION**

Inflorescences, solitary flowers, and bracts -- Inflorescences and the more common solitary position of flowers in this tribe are similar in initiation; with the differences between the two only becoming evident later in their development. In both cases, the flowers and their subtending structures initiate in an inwardly spiral direction. In an inflorescence, each flower initiates in the axil of a bract (floral leaf) having two stipular lobes. Similarly, a solitary flower initiates in the axil of a leaf bearing two stipules. The distinction is that in the inflorescence, as the floral leaves and stipular structures develop, they are different in size, color, or shape from the other foliage leaves and stipules on the plant. The stipular lobes usually become part of the blade of the mature floral bract, sometimes appearing as lobes on the bracts and sometimes indistinct. Since each floral bract initiates prior to the floral apex that it subtends, as does a leaf with a solitary flower, a floral bract is homologous to a leaf. Likewise, the accompanying floral stipular structures are homologous to vegetative stipules.

In the case of *Malachra capitata*, the inflorescence is a capitulum, because the inflorescence axis and the pedicels do not elongate. The floral bracts in this species are broad, larger than the flowers they subtend (but smaller than foliage leaves), and are somewhat showy with a green and white color pattern. Since these flowers lack involucels, the bracts appear to
function as protection and possibly as attraction to pollinators for the entire capitulum.

**Bractlets** -- The involucellar bracts or bractlets are dissimilar to leaves and floral bracts in several ways. Bractlets initiate on the floral apex rather than subtending it, like a bract. It follows then, that the bractlets initiate after the floral apex rather than at the same time or prior to the floral apex. In addition, several to many bractlets develop with each flower; whereas only one leaf subtends each axillary flower or cluster of flowers. Therefore, the bractlets are more likely homologous to sepals than to leaves.

Payer (1857) did not distinguish between floral bracts (which subtend floral apices) and involucellar bracts or bractlets (which occur on floral apices). He treated them both as homologous to leaves and stipules. He reported that the "calicule" (involucel) was formed by "bractées" and their accompanying "stipules". He concluded that "calicules" with numbers other than three, formed by a single flower having more than one "bract" and "stipule" pair, and by two stipules fusing to become one member. He described the pattern of initiation for the "bractées" in *Kitaibelia vitifolia*, *Pavonia hastata*, and *Hibiscus syriacus* with two opposite members arising first, then lateral "stipules" members arising later. If one only looks at a few sporadic stages of bractlet initiation, it is easy to see how this conclusion was made regarding some taxa. I considered it myself, but after looking at numerous micrographs at various developmental stages, it became clear that bractlet initiation follows a helical pattern in the representatives of Malvavisceae. Therefore, the involucel in this tribe is made up of various numbers of bractlets which initiate in a pattern that is helical, with some variation.
Can the bractlets in malvaceous flowers be considered a second set of sepals? It is not unusual for flowers to have extra whorls of organs, such as two whorls of stamens in the legumes (Tucker, 1987); two whorls of sepals and stamens in *Lythrum salicaria* (Cheung and Sattler, 1967); and two petal whorls in some Papaveraceae (Karrer, 1991; Lehmann and Sattler, 1993), Capparaceae (Karrer, 1991), and in *Albizzia* (mimosoid legume)(Ramírez-Domenech and Tucker, 1990; Ramírez-Domenech, 1991). Cheung and Sattler (1967) concluded that the epicalyx in *Lythrum salicaria* was an outer sepal whorl based on morphological, developmental and anatomical similarities to the inner sepal whorl. There are, however, several reasons why the bractlets should not be considered extra sepals in this tribe. First, the bractlets and sepals within a single flower do not necessarily have the same morphological attributes or functions. Second, the bractlets and sepals in the same flower can arise by different initiation patterns (some helical, some simultaneous). Thirdly, the merosity of the bractlet and sepal whorls usually differ. A fourth reason is that the sepals are arranged in a whorl adjacent to the petals, but the position of the involucel relative to the calyx can be variable. In the taxa examined in the Malvavisceae, the involucel was always in a whorl adjacent to the calyx. In the Malveae, however, *Mavella leprosa* (Fryxell, 1988) and several species of *Callirhoe* (Dorr, 1990) and *Anisodontea* (Bates, 1969) have one or more members of the involucel separated from the base of the calyx. The bractlets are described as inserted in a more or less irregular spiral arrangement in a few species of the Gossypieae (*Lebronnecia kokioides, Thespisia beatensis, Thespisia populnea*, and *Hampea rovirosae*) (Fryxell, 1979). The ontogeny of *Callirhoe involucrata var. involucrata*, *Anisodontea X hypomandarum*, and *Thespisia populnea* will be examined in
detail in subsequent chapters; for now, it is sufficient to note that the extra perianth structures in these taxa initiate on the floral apex and thus fit the definition of bractlets. Therefore, since the bractlets can occur vertically spaced on the floral axis or further down on the pedicel, it is unlikely that they can be considered as an extra sepal whorl. If a floral organ is defined as any one that initiates on the floral apex, then these bractlets should be considered as floral organs.

The function of the bractlets can vary. In *Malvaviscus arboreus*, *Pavonia bahamensis*, *Pavonia spinifex*, and *Urena lobata*, the involucellar bracts are narrow, green, and shorter than the petals; thus their main function appears to be for protection in the young floral buds. In contrast, the bractlets of *Pavonia strictiflora* are broad, brightly colored, exceed petal length and likely function as an attractant to pollinators.

In some taxa, the merosity of the bractlets is variable. Merosity in the involucel varies greatly in *Malvaviscus arboreus*, *Pavonia bahamensis*, and *Pavonia spinifex*, all with five or more bractlets. *Pavonia strictiflora* fairly consistently bears four bractlets; rarely only three are produced. Bractlet merosity in *Urena lobata* is very stable, with five bractlets consistently initiated in positions alternate to the sepals.

In all the taxa with involucels, initiation of the bractlets is helical. A bractlet ring meristem, however, is not consistently present among taxa. The involucel appears to initiate on a low ring meristem on the floral apex in *Malvaviscus arboreus*, *Pavonia bahamensis*, and *Pavonia spinifex*; it is unknown if *Pavonia strictiflora* has a bractlet ring meristem (Figs. 2.1, 2.58, 2.72). Paradoxically, *Urena lobata* does not have a bractlet ring meristem and it is the only taxon of the six examined in this tribe that has connate bractlets.
Mode of initiation and subsequent connation are considered two independent processes. Therefore, the presence of a ring meristem does not appear to correlate with bractlet fusion.

Payer (1857) described the members of the "calicule" as all arising as distinct bulges (no ring meristem) and that any connation occurred after initiation. Payer's illustration of *Pavonia hastata*, however, may show the presence of an involucellar ring meristem. He also discussed how the work of Duchartre (1845) alludes to the presence of a bractlet ring meristem which later became separated into primordia. Since the ring meristems, when present, are not always very pronounced, this character can only be determined by viewing the stages of the floral apex just prior to initiation of bractlet primordia.

**Sepals** -- Several physical attributes of the calices are variable among taxa. Calices in all six taxa are five-lobed, but the amount of fusion among sepals varies among the taxa, with *Pavonia bahamensis* having most and *Urena lobata* the least. Height of the calyx (equal, subequal, or exceeding the bracts or bractlets) varies among taxa. Only *Pavonia strictiflora* and *Malachra capitata* deviate from green coloration in the sepals.

Sepal initiation is complicated in Malvaceae, involving the activity of a ring meristem in some taxa. Bractlet number determines the variable number of sides of the pre-sepal apex but does not necessarily predict sepal number. Sepals appear to initiate helically in *Malaviscus arboreus, Malachra capitata*, and the three species of *Pavonia* (Figs. 2.4, 2.41, 2.60, 2.74, 2.86). All of the latter have low sepal ring meristems except *P. bahamensis* (Fig. 2.59), which has a very pronounced sepal ring. *Urena lobata* has simultaneous initiation of the five sepals and there is no clearly definable sepal ring meristem.
Basal fusion of the sepals also appears to occur later in floral development for *U. lobata* than for the other taxa.

There seems to be a transition from helical initiation in the outer bractlet whorls to the simultaneous initiation within each of the petal, stamen and carpel whorls. Order of initiation of the sepals is often an intermediate of the two initiation patterns, with initiation of two subopposite sepals, followed by two or three that are simultaneous or nearly so. The sepal order is helical, but angle of divergence varies from about 170 degrees between the first two, to about 70 degrees for the last three. Length of the plastochron (time interval between initiation of successive similar primordia in an apex) between successive sepal primordia may also vary; one often sees only the first one or two sepals present, or all five, but rarely does one see three or four present. In the case of *Urena lobata*, the early transformation to simultaneous initiation in the sepals may, in part, be due to the stability of the involucellar whorl, which consistently has five bractlets in set positions. Transition from helical initiation in the outer floral organ whorl or whorls to simultaneous initiation in each of the inner organ whorls has also been found in *Theobroma cacao* (Sterculiaceae) (Bayer and Hoppe, 1990).

**Petals** -- Several morphological characters of the petals are variable among Malvavisceae members. A variety of color (pink or lavender, greenish-yellow, yellow, orange-yellow, red, and rarely white) is found in the pentamerous corolla. Petal height exceeds the sepals in all taxa except *Pavonia strictiflora*, in which petal height is equal, slightly exceeds or is slightly less than sepal height. With the exception of *P. strictiflora* and *Malachra capitata*, the petals exceed the height of the bracts or bractlets.
Tubular (i.e. not flaring) corollas form in three taxa, *Malaviscus arboreus*, *Pavonia strictiflora*, and *Pavonia bahamensis*. According to Endress (1994), tubular flowers may result by congenital or postgenital fusion of petals, by confinement of free petals by the calyx, or by incomplete opening of a contort choripetalous corolla. The latter pattern applies to *Malaviscus* and *P. bahamensis*. In the case of *P. strictiflora*, the tubular flowers are likely formed by both confinement by large, stiff bractlets and the sepals and by incomplete opening of the petals.

Petal contortion occurs in all the taxa examined in Malvaviscaceae. Corolla twisting is found not only in Malvaceae, but also in Bombacaceae, Sterculiaceae, Cochlospermaceae, Linaceae, Caricaceae, Palmae, and Tiliaceae (Davis and Selvaraj, 1964). The ratio of right-handed to left-handed flowers of a species in any of these families is about 1:1 (Davis and Selvaraj, 1964). Additionally, the androecial and gynoecial columns twist in *Malaviscus arboreus*. An auricle is found on one side of each petal base in *M. arboreus*; the presence of such auricles is characteristic of the genus *Malaviscus*.

**Androecia** -- Merosity of the stamens varies between taxa and even within a species. *Malachra capitata* can have as few as ten stamens and *Pavonia strictiflora* can have as many as 50 stamens. In general, the numbers of stamens are usually multiples of five. The stamens are congenitally fused, having been initiated on a ring meristem. Congenitally united stamens are common in Malvales and Fabales and occur in several Magnoliidae (Endress, 1994), although the mechanisms creating fusion differ greatly among these taxa. A more detailed discussion of stamen proliferation will be given in Chapter 3.
Radial symmetry prevails in the androecium, in that the anthers are displayed radially around the columns in all taxa except *Pavonia bahamensis*, which becomes zygomorphic. In *P. bahamensis*, the filaments at maturity twist to one side so that the anthers are presented on one side of the column, (i.e. are secund); it should be noted that the flowers are positioned with the longitudinal axis oriented horizontally in this taxa. Although not typical of Malvaceae, zygomorphic androecia are found in some other species of *Pavonia* (Fryxell, 1988, 1999) in *Hibiscus clypeatus* (Fryxell, 1988).

Overall elongation of the androecial column plays a role in the presentation of the anthers. Longer columns have the filaments and anthers concentrated in the upper portion (top 1/3 or less) of the column. Androecia that are shorter (as in *Malachra capitata* and *Urena lobata*) have filaments and anthers presented nearly throughout the column. Therefore, elongation of the androecium appears to occur mostly in the basal area of the column.

There is variation in the staminal filaments among tribal members. *Urena lobata* lacks elongation of the filaments so that the anthers are subsessile (Fig. 2.123). The mature filaments in *Malaviscus arboreus* are retrorse (Fig. 2.35). A slight amount of retrorseness also occurs in the filaments of *Pavonia strictiflora*. Stamens can be attached singly or in pairs to the staminal column. Even though all of the taxa examined in this tribe have at least some stamens resulting from bifurcation of common primordia, not all of the taxa have some stamens diverging in pairs. Filaments diverge singly in *M. arboreus* and *Pavonia bahamensis*. In the other taxa, the filaments diverge singly and in pairs. Most of the paired filaments are placed one above the other (or obliquely so) on the column (Figs. 2.54, 2.79, and 2.123). It appears that the number of paired stamens per column is equal to or less than the
number of stamens that results from bifurcations. It is reasonable to assume that bifurcation of common stamen primordia is responsible for stamen primordia that are initially joined and that column elongation may be the factor that determines if these particular stamens remain in pairs or separate vertically on the column. Developmental age of the paired stamen primordia at the time of column elongation and the total amount of column elongation may be the factors that determine if the ontogenetically formed pairs will be subsequently separated in the mature flower.

Position of the sterile teeth is variable in this tribe. In *Malachra capitata* the teeth are opposite the petals (Fig. 2.98), in *Pavonia strictiflora* and *Urena lobata* the teeth are alternate to the petals (Figs. 2.47, 2.110), and in the other taxa the teeth are positioned opposite and off-center to the petals (Figs. 2.21, 2.65). The difference seems to be due to how stamen primordia initiate and the location of the remaining tissue is on the ring meristem that will ultimately produce the sterile teeth. Van Heel (1966) also found that the position of the sterile teeth varied in Malvaceae. He reported that the sterile parts were alternate to the petals in taxa such as *Kitaibelis*, *Sphaeralcea*, and *Urena*, and opposite the petals in taxa such as *Abutilon*, *Hibiscus*, *Pavonia* (it is assumed this excludes the species formerly in *Goethea*, i.e. *P. strictiflora*), and *Malvaviscus*. Saunders (1936) characterized all of the sterile teeth in Ureeneae (including *Pavonia*, *Malvaviscus*, and *Goethea*) and in Hibisceae as terminations of antepetalous sectors of the androecial tube and thus to be in a position opposite the petals. On this aspect of teeth position, my research on members of the Malvaviscceae is in agreement with van Heel's work and contradicts part of Saunders'. The sterile teeth in flowers of members in this tribe can be located alternate with or opposite to the petals.
The petal-stamen ring meristem -- A petal-stamen ring meristem forms in all taxa examined in the tribe Malvavisceae. On this ring five common petal-stamen mounds initiate simultaneously in positions that are alternate and interior to each of the sepals. The common petal-stamen mounds are actually mounded sectorial regions on the ring meristem. From each common mound a petal primordium becomes distinct, at the same time that a common stamen primordium emerges. The petal primordia and the first set (and sometimes subsequent sets) of common stamen primordia appear to initiate separately in their shared sectorial regions of the ring. Throughout stamen initiation, the stamen groups (those that arose from the same common petal-stamen mound) stay basically on the same radius as their associated petal except in *Malachra capitata*. Petal growth is retarded until all of the stamens have initiated.

The ring meristem in Malvavisceae appears to result from the early expansion of the sectorial region of the floral apex that controls both petal and stamen production. Adnation of the petals to the androecium and connation among stamens are, therefore, achieved in part by congenital fusion, and in part by intercalary growth below the area of attachment.

The formation of the ring takes place in a series of steps. The changes observed are in topography (surface form) from a convex meristematic apex, to a meristem ring around the meristem apex, to a state where the ring bears five mounds, to one where each of the five mounds starts organ initiation. At each step, the meristem becomes more specialized in function for a particular set of organogenetic events. While there are probably cellular differences internally during this series of changes, such as differing division rates and
differing planes of cell division, we have inadequate tools to determine those at present.

Payer (1857) described malvaceous flowers with ring meristems, "volcanoes," on which petals and stamens form, but with the petals appearing before the stamens. He did not describe the appearance of common petal-stamen mounds prior to petal and stamen initiation on the ring. He characterized the androecial ring meristem as divided into ten (only five in *Malvaviscus*) "sectors" separated by grooves and that each "sector" produced a series of stamens. Since he did not describe or illustrate all the stages of androecial development, I believe he missed the five common-stamen mounds or sectorial regions that occur very early on each ring meristem. What he described as "ten sectors" are actually primordia (often common primordia) that result at slightly later stages of development. He even depicted some of these as being alternately large and small, which would not be uncommon for two different sets (each composed of five members) of primordia that were initiated at different times.

Van Heel (1966) described *Urena lobata* with a "slight central depression" which "delimitates a peripheral wall" on the pre-petal apex. The corner parts of this wall (alternate to the sepals) are elevated. He reported that unequal elliptical staminal buttresses develop on either side of the petal radii. Upon this wall and outward from these staminal buttresses, the five petal primordia initiate and "somewhat later some stamen primordia originate". So, he basically described a petal-stamen ring meristem, but it is unclear if he was alluding to common petal-stamen mounds. He also specified that petal initiation precedes stamen initiation in *U. lobata*; this is contrary to the simultaneous initiation described in the present research. In general, he
characterized the petals as growing from the lower outer base of the staminal buttress before any stamen primordia appear, in the Ureneae and Hibisceae. In Malveae (including the former tribe Malopeae), van Heel determined that the petals arise after some of the stamen primordia have initiated.

Sattler (1973) doubted the existence of a meristem ring in Malvaceae. He did not see formation of a petal-stamen ring or common petal-stamen mounds in *Alcea rosea* or in *Malva neglecta* (Malveae). In both, he reported that adnation of the petals to the androecium occurs later by growth in the zone below the petals. In *A. rosea*, he saw the initial five stamen primordia first, then formation of a stamen ring by interprimordial growth. In *M. neglecta*, he described the androecium initiated first as a ridge, then primordia appeared. Differences between my interpretations and that of Sattler may be due to taxon differences, or to his use of a different technique, which does not give the same resolution as SEM. Also, observation of common petal-stamen complexes can be very difficult and critical stages are often missed because the primordia divide rapidly and the petals sometimes develop very slowly (Ronse Decraene, Clinckemaillie, and Smets, 1993). In my chapters 3 and 4, further studies utilizing SEM will help to clarify patterns of floral ontogeny in the sister tribes.

Common primordia, as opposed to discrete organ primordia, have been reported in a diverse array of taxa (Tucker, 1989). Common petal-stamen complexes have been reported in at least 22 plant families (Sattler, 1967; Sundberg, 1982a, b; Tucker, 1989; Ronse Decraene, Clinckemaillie, and Smets, 1993; Evans and Dickinson, 1996). According to Tucker (1989), *Pisum sativum* (Fabaceae) flowers are pentamerous but only four common petal-stamen primordia initiate, three opposite to sepals and one alternate to the
Two of these common petal-stamen primordia each form three primordia and two of them each form two primordia. Tucker explained that in *P. sativum* a ring meristem was not involved. Sundberg (1982a, b) found that in *Cyclamen* (Primulaceae), the five common petal-stamen primordia initiate simultaneously and alternate with the five sepals (as in Malvavisceae), but there was no mention of a ring meristem forming first. It would seem then, that common primordia may initiate in different ways in different taxa and are not necessarily dependent upon prior formation of a ring meristem.

Overlap in time of initiation (superposition) of two different whorls, especially stamens and petals, is not very unusual (Decraene, Clinckemaillie, and Smets, 1993). According to Decraene, Clinckemaillie, and Smets (1993), petals and stamens normally arise as free primordia even when they are superposed; but that superposition is a prerequisite for what they term "stamen-petal complexes" in Magnoliatae. Tucker (1989) stated that the common primordia in *Pisum sativum* can be viewed as resulting from precocious fusion among organs as a consequence of overlap in time of organ initiation. Superposition with the carpel whorl can also occur. In *P. sativum* (Tucker, 1989) carpel initiation overlaps with petal and outer stamen initiation. In species of both *Cyclamen* (Sundberg, 1982a, b) and *Crataegus* (Rosaceae) (Evans and Dickinson, 1996) all of the stamen primordia are initiated before carpel primordia are initiated. In Malvavisceae, although overlap in time of organ initiation occurs, it occurs long after initiation of the petal-stamen ring meristem and the common petal-stamen mounds. The petals overlap in initiation with the first set of stamens, and carpels initiate during the proliferation of stamens.
Endress (1994) characterized that in flowers with a ring-like androecial mound, the gynoecium appears before the individual stamens or at least before the last stamens (the latter is the case for Malvavisceae). This delay in initiation of the individual stamens allows the floral apex to expand, so that the androecial part of the floral apex is separated from the gynoecial part by a furrow and proliferates in the form of a ring-mound.

The formation of an androecial ring meristem is not that unusual, but formation of a ring for petals and stamens is unusual. This combined with common petal-stamen mounds and primordia that initiate organs in several directions in associated sectorial regions on the ring meristem is unique. Centrifugal stamen initiation on a ring meristem has been reported for taxa in the Malveae (van Heel, 1966; Sattler, 1973; Ronse Decraene and Smets, 1992, 1993) and centrifugal or centrifugal-lateral in some of the sister families in Malvales (Ronse Decraene and Smets, 1992). Many other angiosperms give rise to many stamens from ring meristems in one direction or even two, but not three (Ronse Decraene and Smets, 1992; Endress, 1994).

The petal-stamen ring meristem characterizes floral ontogeny of Malvavisceae. This is the first comparative study of floral development in taxa of this tribe using SEM. Floral ontogeny (mostly using techniques other than SEM) of various members of other malvaceous tribes has been published, in some of which the authors are non-committal about presence of a ring meristem preceding petal and stamen initiation. Comparisons among malvaceous tribes, to be made in subsequent chapters, are clearly needed to elucidate this question.

Stamen proliferation and bifurcation -- In this description of stamen proliferation, the sets of stamen primordia are numbered (first, second, third,
etc.) according to the order in which they initiated. The terms primary and secondary primordia were not used here, to avoid confusion. Endress (1994), in describing *Kitaibelial*, referred to the initial common stamen primordia on the ring as primary primordia and referred to all stamen primordia that initiate thereafter (regardless of their numbers, position, or order of initiation) as secondary primordia. Sattler (1973) in looking at two taxa in the Malveae, used the term primary for the first set of stamen primordia, secondary for all ten primordia that result from the lateral bifurcation of the primary, tertiary for all primordia that initiate centrifugally from the secondary (regardless of the number of outward sets and their order), and quaternary to represent all primordia that result from the lateral division of tertiary primordia. I prefer to go into more detail on how the secondary and tertiary primordia arise.

All of the taxa with complete staminal initiation known in this study have a combination of lateral, centrifugal and centripetal initiation of stamen sets. Stamens generally initiate in sets of five with simultaneous initiation within each set. There is often overlap in time of initiation among the stamen sets; i.e., bifurcations of two or three different sets may occur at the same time. Bifurcation of common stamen primordia is partly responsible for the large number of stamens in these taxa, although the ontogenetic sequence and timing varies for each taxon. In *Malvaviscus arboreus*, the directions of stamen proliferation are: one lateral, one centrifugal, then two centripetal. The first, second, and third sets of staminal mounds (Figs. 2.10 - 2.12) lack the elongated peanut-shape and slightly elevated bases that would clearly demark bifurcation of common primordia. Therefore, it appears that these three sets of primordia initiate independently (but in close association with each other) from a common sectorial region on the ring meristem. The fourth and fifth sets
of stamen primordia clearly result from bifurcation of common primordia (Figs. 2.13 - 2.15). The first and second sets of common stamen primordia subsequently bifurcate, but the third does not. In *Pavonia strictiflora*, the directions of stamen proliferation are: one lateral, two centripetal, one centrifugal, two centripetal, then two oblique centrifugal. Only the sixth through the ninth sets of stamens clearly result from bifurcation of common primordia. The directions of stamen proliferation in *Pavonia bahamensis* are: one lateral, one centripetal, one centrifugal, and three oblique centrifugal. The fifth, sixth, and seventh sets of stamen primordia result from bifurcation. In *Pavonia spinifex*, bifurcation of common stamen primordia yields the sixth, seventh, and eight sets of stamen primordia. Bifurcation of stamens occurs quite early in *Malachra capitata*, with the second set of stamen primordia clearly resulting from bifurcation of the first set (Figs. 2.89 - 2.91). The direction of this division is laterally-centrifugal. In *Urena lobata*, the directions of staminal proliferation are one lateral and one centrifugal concurrently, then one oblique centripetal, and sometimes this is followed by oblique centrifugal divisions. Any stamen sets beyond the third set in this species are the result of bifurcations.

The staminal bifurcations can be initially uneven (with unequal-sized lobes on the peanut-shaped common primordia) as in *M. arboreus* (Fig. 2.15), or the lobes can be equal in size as in *Malachra capitata* (Fig. 2.91). Even though Payer (1857) did not describe it, his illustrations of *P. hastata* show unequal division of some common stamen primordia. Van Heel (1987) also found unequal division of common stamen primordia in *Actinidia chinesis* (Actinidiaceae). In most of the other taxa in which bifurcation of a common
staminal primordium has been reported, the resulting two lobes are equal in size (Bayer and Hoppe, 1990; Ronse Decraene and Smets, 1993).

Other researchers have described bifurcation of stamens in Malvaceae flowers. Payer (1857) reported both lateral and radial bifurcations in *Pavonia hastata*. Payer explained that the oldest stamens occurred at the top of the androecial ring and the youngest at the base (centrifugal). He did not illustrate or describe a complete ontogenetic series for the flowers he examined. It appears, however, that what he described as radial bifurcations of some of the stamens at the top of the column in *P. hastata* may actually be centripetal divisions, which would mean that at least in the case of Malvavisceae, not all of the youngest stamens occur at the base of the androecial column. The assumption of centripetal division is based on my interpretation of his illustration in which the primordia elongate in an inward direction, with bifurcation resulting in interior lobes that are initially smaller than the outer lobes. Saunders (1936) believed that the whole number of fertile stamens corresponds to a single whorl of five antepetalous members, the primordia of which have undergone a primary collateral splitting and thus given rise to \(10 - \infty\) half stamens. Van Heel (1966) described some of the stamen pairs in Malvales as resulting from serial splitting of a stamen with primordia originating in centrifugal rows.

All of the anthers are bisporangiate (unilocular). Attempts have been made by previous researchers to attribute the formation of these "half anthers" to the bifurcation of common stamens. Payer (1857) attributed the unilocular anthers in *Lavatera olbia* as having arisen from division of each bilocular stamen into two. Yet in *Pavonia hastata*, he described the stamen primordia dividing more than once without any change in anther locule number.
Saunders (1936) looked at the vascular system in the androecium. In *Corydalis* (Fumarioideae), she stated that "if the vascular complement proper to a floral member is halved before the bundle is fully organized and delimited from the vascular elements appropriated to other whorls, and if the two halves do not reunite, then the corresponding floral member will be replaced by two separate half members." In the Fumarioideae, after the first halving, there is no subsequent division of the bundles. Therefore, only one pair of half stamens replaces what would be a whole stamen. Saunders further claimed that subsequent splitting of half strands after they have become isolated (i.e. after the determinate phase has been reached), will not result in further fractionization of the organs, but in the multiplication of the product of the original bipartition. She concluded that in Malvaceae, repeated division usually occurs after the first halving, thus explaining why a large number of half stamens are produced in place of a single whole stamen. Rao (1952) was not convinced by Saunders' evidence. He found that the staminal traces in members of the Malvales divide into three bundles regardless of whether they make dithecous or monotheceous stamens; the only difference he reports is the level at which branching occurs. He was not swayed by her argument that only the primary and not the secondary division results in fractionalization. Van Heel (1966) characterized that half stamens were actually the result of serially split stamens, the branches of which are inserted on the androecial tube. He justified this by the occurrence of other half stamens that occur distinctly in pairs (paired divergence of filaments). He did not attempt, however, to directly correlate the single or paired condition of the stamens on a mature flower with early ontogeny. Both Saunders' and van Heel's theories did not adequately take into account how the bisporangiate condition arises in
stamens that do not result from a bifurcation, i.e. primordia that arise independently in their sector of the ring meristem and never undergo a division. In addition, if the bisporangiate condition was the result of bifurcation, one would expect to always have an even number of stamens; this is not always the case. For example *Malvaviscus arboreus* typically has 25 stamens, all with bisporangiate anthers. This odd number results from the last five staminal primordia not bifurcating. Ronse Decraene and Smets (1993) described a similar type of dedoublement in *Theobroma cacao* (Sterculiaceae), in which only one of the two original stamen whorls bifurcates. Therefore, according to my observations with the tribe Malvavisceae, the bisporangiate condition does not correlate with the bifurcation of stamen primordia. Some stamen primordia do not bifurcate and some bifurcate once, yet all of the anthers are typically bisporangiate.

The direction of bifurcation in the tribe Malvavisceae may be, in part, a function of crowding. In *Malva neglecta* and *Alcea rosea* (Sattler, 1973), *Abutilon megapotamicum* (Ronse Decraene and Smets, 1993), *Theobroma cacao* (Bayer and Hoppe, 1990; Ronse Decraene and Smets, 1993), and *Kitaibelia vitifolia* and *Malope trifida* (van Heel, 1995) some of the stamen primordia appear to result from bifurcations; and these bifurcations occur in a lateral direction (In some of these taxa, the determination of bifurcation and the direction was based on my observations of their figures). In these taxa the androecial ring or the staminal floral apex appears relatively large in surface area in proportion to the stamen primordia. In the Malvavisceae, the androecial ring is relatively small. This lack of space on the androecial ring may be responsible for forcing staminal divisions to occur centripetally, centrifugally, or at oblique angles in members of the Malvavisceae.
Torque created by petal primordia set obliquely or by petal contortion is not a likely factor in determining the direction of stamen bifurcation. If petal torque was responsible, one would expect all the bifurcated sets of stamen primordia in a given flower to be oriented in the same oblique direction. This is clearly not the case. Sets of bifurcating common stamen primordia in a malvaceous flower can be oriented in different oblique directions (Figs. 2.46, 2.63, 2.76). A more detailed discussion of dedoublement, stamen splitting, and multiple groups of stamens will be given in Chapter 3.

Gynoecia -- All of the taxa examined in tribe Malvavisceae have floral structures with ten styles and ten stigmas terminating five locular ovaries with one ovule per locule. The ovaries are superior with axile placentation and capitate stigmas. The overall height of the gynoecial column exceeds the androecium in all taxa and exceeds the corolla in all taxa except *Malachra capitata* and *Urena lobata*. The styles diverge from the top of the column radially. In *Pavonia strictiflora*, the upper portion of all of the styles appear to bend slightly in the same direction (lack of floral material makes this inconclusive).

There were discernible differences in height between the sterile and fertile carpels (styles) within the gynoecial columns of all of the taxa except in *Malachra capitata* and *Urena lobata*. In the former case, the-sterile carpel members were taller; in the latter, all styles were approximately equal in height. Van Heel (1978) also found that in Ureneae (Malvavisceae) the shorter stylar members belong to the fertile carpels. He made no exception to this, however, for *U. lobata*, and he did not examine *M. capitata*.

Carpels initiate as two sets of five with simultaneous initiation within each set. No ring meristem appears to be involved in carpel initiation.
The petal-stamen ring was completely expended by initiation of stamen teeth. The two carpel sets composing the gynoecium initiate at different times and from independent areas of the apex (i.e. not from common primordia, common mounds, or from a shared ring meristem, as is the case in the androecium). So in this respect, the gynoecium may be considered to consist of two carpel whorls; i.e. each set equals a whorl. It is important to note, however, that the sets of alternating carpels in the gynoecium initiate equidistant from the central floral axis; one set is not interior to the other. So, for lack of a better term, the two sets (whorls) of carpels share the same "spatial whorl".

Position of the first set of carpels differs among taxa. The first set of carpels consistently initiates alternately to the sterile teeth. However, because the position of the teeth (alternate or opposite in relation to the petals) varies among taxa, the position of the first set of carpels also varies among the taxa (alternate or opposite in relation to the petals). In *Malaviscus arboreus* and *Malachra capitata* the first set of carpels are alternate to the petals. *Pavonia bahamensis* has the first carpels alternate and off-center to the petals and *Pavonia strictiflora* and *Urena lobata* initiate carpels opposite to the petals. In *U. lobata*, the first set of carpels is fertile. In all other taxa where carpel initiation is known, the second set of carpels is fertile.

My observations differ somewhat from previous ones as to how the carpels initiate in members of the Malvavisceae. Payer (1857), Saunders (1936), and van Heel (1978) describe initiation of two sets or whorl of carpels in the gynoecium. Payer's (1857) illustration of *P. hastata* shows the ten carpel primordia as equidistant from the central floral axis, similar to my research. In contrast, Saunders (1936) and van Heel (1978) described one set of carpels as inner and the other as outer. Payer (1857) did not discuss
whether the first or second formed set of carpels was fertile. Baillon (1875) described *Urena* and *Malaviscus* with fertile carpels or "ovary cells" opposite the petals and *Pavonia, Malachra*, and *Goethea* with fertile carpels alternate to the petals. I differ with him in that fertile carpels in *Malachra* are opposite the petals and in *Pavonia bahamensis* they are almost opposite. Saunders (1936) stated that the outer carpel whorl is sterile and the inner is fertile. In contrast, Van Heel (1978) believed that the first outer five carpels are fertile and the second inner set of carpels is sterile. With the exception of *Urena lobata*, I found that the second set of carpels is fertile, not the first.

Other interpretations of carpel initiation in members of the Malvaceae involve a gynoecial rim or common carpel primordia. Sattler (1973) indicated that the carpels initiate as a single whorl in two taxa in the Malveae; a gynoecial rim was described on which carpel primordia initiate in *Alcea rosea*. In *Malva neglecta*, he described "primary" gynoecial primordia that grow into a ridge and subdivide into carpel primordia. In *Kitaibelia vitifolia* (Malveae) (Endress, 1981) the carpels are said to initiate as five primordia that each subdivide into ten secondary primordia, yielding a total of 50 carpels. In the gynoecia in flowers of the Malvavisceae, I found no evidence of a ring meristem or of common primordia.

The development of the sterile carpel bases is limited to different degrees, according to the species. None of the sterile carpels form functional locules. However, in *Pavonia strictiflora* and *Urena lobata*, the sterile carpels form dimples and then small crevices (Figs. 2.50, 2.51, 2.114, 2.116). In *Pavonia spinifex* only dimples form (Fig. 2.77). No evidence of indentation can be discerned in the other taxa (Figs. 2.24, 2.67, 2.96). The side walls of the fertile locules in the three species of *Pavonia* appear to be joint products of
both the sterile and the fertile carpels (Figs. 2.52, 2.68, 2.77). In *Malaviscus arboreus* and *Malachra capitata* the sterile carpels seem to be primarily responsible for the lateral walls of the locules; this is due to the inward growth of the young sterile carpel bases (Figs. 2.26, 2.97). Only in *U. lobata* are the locular walls primarily formed by fertile carpels (Fig. 2.116).

Similarly, van Heel (1978) described that *Pavonia spinifex, Pavonia hastata,* and *Malaviscus arboreus* lack sterile locule formation or almost so, and that *Urena lobata* and *Pavonia praemorsa* form small locules. He also noted that the sides of the locules are developed by the lateral flanks of carpel primordia and that the roofs of the locules are formed by the overarching top parts of the primordia. Van Heel (1978) explained that in all the taxa he examined, the bases of the sterile carpels are situated higher on the apex than those of the fertile carpels. Payer (1857) determined that in the gynoecium of each *P. hastata* flower, only five carpel primordia invaginate to form locules; the five other carpel primordia that alternate are sterile and persist in some way in partition walls. According to Saunders' (1936) theory on carpel polymorphism, the pistil consists of five 'fertile carpels' (that make up the 'septs' and 'placentae') and five 'sterile carpels' (that make up the locules and their walls). In her theory, normally only the 'sterile carpels' have styles, but in Ureneae the 'fertile carpels' also have styles. My research and van Heel's (1978) disprove Saunders' theory by showing that in some taxa, the sterile carpel primordia do form locules (or at least partial locules), but do not develop further.

Early carpel growth varies among taxa. In *Malaviscus arboreus, Pavonia bahamensis,* and *Pavonia spinifex* the tips of the young sterile carpels converge inward more so than in the fertile carpels (Figs. 2.29, 2.69, 2.78).
In the other three taxa, the young sterile and fertile carpel tips are in a peripheral ring with each carpel equidistant from the center (Figs. 2.53, 2.97, 2.118). Van Heel (1978) stated that the proximal parts of the styles consist of five fertile carpel parts in the middle and five regions of tissue leading to the sterile carpel parts in the periphery. The distal stylar parts, however, he said consist of five sterile carpel parts which have grown in the centripetal direction and fertile carpel parts in the periphery. I found no evidence to support van Heel's view; the sterile carpels consistently occupied the center of the stylar column in the taxa previously described.

Gynoecium initiation usually encompasses the entire remaining floral apex in angiosperms (Endress, 1994). In the representatives of the Malvavisceae, the floral apex was not incorporated into the gynoecial primordia; a small apical residuum remains in the center of the gynoecial whorl. Van Heel (1978) also noted in Ureneae that the regions of the apex internal to the carpel primordia do not take part in the inward development of the primordia. Endress (1994) also found that in some cases where a large number of carpels are initiated (as in Kitaibelia), that the central region of the apex may not be incorporated into the gynoecium.

The stigmas differentiate before the styles emerge beyond the androecial column in Malvaviscus arboreus, Pavonia bahamensis, and Malachra capitata (Figs. 2.34, 2.35). In Urena lobata the stigmas differentiate after the styles surpass the androecium (Fig. 2.120). This character was not determined for the other taxa.

The mature ovary surface in Malvaviscus arboreus is relatively smooth, with not much evidence of lobing (Fig. 2.37). The surface of the ovaries of the other taxa all appear five-lobed to various degrees (Figs. 2.56, 2.69, 2.80,
The mature ovary surface in *Malachra capitata* is rugose with trichomes (Fig. 2.99). *Pavonia spinifex* has trichomes, basal lobes, and apical ridges on each mericarp of the ovary (Fig. 2.81), and in *Urena lobata* the surface is covered with young spinal protuberances and trichomes (Fig. 2.122).

**Nectary, pollen, and fruit** -- All of the taxa examined have trichome nectaries located on the inner base of the sepals. According to Endress (1994), nectaries located on either the inner or outer surface of the sepals are found in Malvales and in *Thunbergia* (Acanthaceae). Trichome-type nectaries are relatively rare but are characteristic of Malvales and Dipsacales, and also occur in some Asclepiadaceae, Scrophulariaceae, Cucurbitaceae, and Verbenaceae.

The fruit types are all dry schizocarps except for *Malaviscus arboreus*, which has fleshy schizocarps (berries), and *Pavonia strictiflora*, in which the fruit type is unknown. The schizocarpous fruits are basically oblate, with the height less than the width. In *M. arboreus*, the fruit height is greater or equal to the width. The fruit in *Pavonia bahamensis* has broad lateral wings, and in *Malachra capitata* it has reticulate veins. *Pavonia spinifex* has rugose fruit with three retrorsely barbed spines per mericarp. *Urena lobata* has numerous retrorsely barbed spines per mericarp (Figs. 2.125, 2.126). According to Endress (1994), similar retrorsely barbed spinal protrusions are found in the fruit of *Rulingia pannosa* (Sterculiaceae).

All of the pollen examined in tribe Malvavisciaceae is spherical or spheroidal and polyporate. *Pavonia strictiflora* is unique in having smooth pollen grains (Fig. 2.57). All of the other taxa have spiny pollen (Figs. 2.36, 2.71, 2.82, 2.100, 2.124). Spheroidal, polyporate, and spiny pollen grains
have also been reported for other members of the Malvaviscæae (Christensen, 1986).

**Vascular structure in the androecium and gynoecium** -- While no studies were made here of the vasculature, the subject has provided valuable evidence concerning floral architecture and homologies. Several papers have examined floral vasculature in Malvaceae. Rao (1952) looked at the vascular traces in *Malvaviscus arboreus*. He found that the petal-stamen traces were conjoint, alternate and off-center with the sepal traces, and form a ring. At the level of separation of petals from the staminal tube, five pairs of traces can be seen inner to the bases of the petals. From these five traces, stamen bundles are given off alternately. After the stamens form, five remaining traces supply the staminodial teeth. A number of bundles in a ring supply the receptacular stele after separation from the petal-stamen trunk. Ten of these bundles bend inward and function as the marginal traces for the ten carpels. The marginal traces continue into the styles.

Van Heel's (1978) description of the vascular system in Ureæae also described combined petal-stamen bundles and ten pistillar traces. He claimed it is possible that above the level of divergence of the sepal and petal-stamen traces, a closed stele is reconstituted, which is five-angled in the petal radii and from which the ten gynoecial traces originate. This is dependent on the amount of apical growth intervening between the origin of the sepals and petal-stamen primordia and also the carpel primordia. He claimed that if there is a lag between the two, a stele will be reconstituted. Van Heel continued with a description of how the stylar bundles at first appear to all arise from the fertile carpels, but later it is evident that the bundles are shifted slightly sideways, and are nearer to the boundaries between the fertile carpels and...
the tissue which passes upwards into the sterile carpels. At higher levels, 
these bundles form commissural bundles between the fertile and sterile 
carpels. In the style, these bundles develop only after lateral fusion of the 
components has eliminated morphological boundaries between the two sets of 
carpels. At higher levels, each of these bundles divide in two to enter the two 
adjacent stigmatic branches. Van Heel claimed that a vascular supply to the 
sterile components is effectuated in this way, which would otherwise not be 
available. The shared vascular bundles appear to support a close 
developmental relationship between petals and stamens. In addition, the 
homology is supported between stamens and the stamen teeth, based on 
similar vascular supply.

Syncarpy -- The formation of separate styles by both sterile and fertile 
carpels of the same ovary is rare, but it has been found in some of the 
Eriocaulaceae and occasionally in *Eschscholzia* (Papaveraceae) (Saunders, 
1936). The development of a second whorl of carpels, which together with the 
first whorl form one pistillary structure, is known for *Punica* and *Siphonodon* 
(Croizat, 1947 via van Heel, 1978) and the Navel orange (van Heel, 1978).

One advantage of a syncarpous gynoeicum is the presence of a 
compitum, a connection between the carpels which allows pollen tubes from 
grains germinating on any stigma or part of the stigma to fertilize ovules 
belonging to more than one carpel. This facilitates the even distribution of 
pollen tubes among the carpels (Carr and Carr, 1961; Endress, Jenny and 
Fallen, 1983; Endress, 1994). Van Heel (1978) described this compitum in 
members of Ureneae (Malvaviscæae). Ten transmitting strands lead from the 
stigmatic branches. Downward they fuse into one cylinder of pollen tube 
transmitting tissue in the middle of the stylar column. In most taxa, five
transmitting strands diverge lower in the column from the cylinder (one to each of the five fertile carpels). In *Pavonia praemorsa* and *Urena lobata*, one to five alternating strands can form that terminate blindly downwards, in addition to the usual five strands. He believed that the blind strands were due to the initial formation of locules in the sterile carpels of these species.

The gynoecium in members of the Malvavisceae may represent a transition from ten fertile carpels in a hypothetical ancestor to five sterile and five fertile carpels. The discovery of blind pollen tubes leading to the more developed sterile carpels from the compitum in addition to the range of locule development found in different taxa in the tribe are evidence of this transition. The mention of occasional fertile carpels in place of the steriles in *Pavonia praemorsa* and *Urena lobata* (van Heel, 1978) is also added proof of such an ancestry. This reduction of locule number, with the maintenance of the ten stylar system, allows for the increased possibility of pollen landing on the stigmas and thus more chances of the five ovules becoming fertilized. The reduced number of ovules could be a benefit with increased seed size.

Van Heel (1978) concluded that the aberrant fruit (which results from both fertile and sterile carpels) in Ureneae (Malvavisceae) represents an evolutionary transitional state. He stated that "capsular fruits with many seeds, as in Hibisceae and in the Malvales as a whole, are considered primary, and fruits with many monospermic parts advanced, then the case of Ureneae may represent a transitional state". It should be noted that members of the Hibisceae generally have a five-merous gynoecium resulting in a capsular fruit with five many-seeded locules, and members of Malvavisceae have a ten-merous gynoecium resulting in a schizocarpous fruit with five one-seeded locules. Therefore, if I am interpreting the above quotation correctly,
van Heel's hypothetical ancestral fruit would have five locules with many seeds in each, and the advanced fruit would contain ten locules with one seed in each. Hopefully, the cladistic analysis of the tribes in a subsequent chapter will lend some insight about the evolutionary pathways of the gynoecial forms and fruit types.

Comparative ontogeny and characterization of Malvavisceae --

The currently used morphological floral diagnostic features that distinguish the tribe are supported by findings of the current work. There is a ratio of two styles per mericarp, fruits are schizocarps, there are ten free styles in the gynoecium, and five teeth terminate the staminal column. The statement of "two styles per mericarp", however, might lead one to presume that one sterile and one fertile style are allocated to each mericarp, which is not the case. The condition is ontogenetically produced by the initiation of two sets of five carpels in the gynoecium and by partial inhibition of one set, with suppression of locule development. So perhaps a better way to phrase it would be: a ten-merous gynoecium with a reduction in locule or mericarp number to five. The five apical androecial teeth are formed from the remains of a petal-stamen ring meristem. Their position, with relation to the petals, varies according to where the space available on the ring meristem after stamens have initiated.

The six taxa examined in this research have not been in question as far as their taxonomic position in the Malvavisceae. Therefore, the ontogenetic characters of these taxa can be used as a basis for characterizing the tribe. Flowers in the tribe Malvavisceae generally have bractlets, which initiate in a helical pattern. The merosity of the bractlets can be fairly fixed in some taxa or highly variable in others. Those taxa that lack bractlets have a floral bract subtending each flower. All member of this tribe have a five-lobed calyx.
Depending on the taxa, sepal initiation is either helical or simultaneous. A ring meristem may or may not precede initiation of bractlets and sepals, but is always present before petals and stamens initiate. In fact, the same ring meristem is shared by the petal and stamen primordia. In each flower, five common petal-stamen mounds initiate on a ring meristem in a position that is alternate and interior to the sepals. From each of these common mounds, a petal primordium initiates in an alternate or off-alternate position to the sepals and concurrently a common stamen primordium initiates in a varying position relative to the position of the petals and sepals. Stamen proliferation precedes in a combination of lateral, centripetal, and centrifugal directions. Some of the stamen primordia initiate independently on the ring meristem and other result from bifurcation (often uneven) of common stamen primordia. Initiation within the petal whorl and within each of the sets of five stamens is simultaneous. The stamen group may be radially aligned or not with its associated petal (the petal that shared the same common petal-stamen primordia as the stamen group). The mature petals are distinct, adnate to the androecium, and may or may not have auricles. The stamens are ontogenetically fused and as the remains of the ring meristem elongate vertically, a column forms. At the top of the column, five sterile teeth form in variable position with regard to the petal position. Filaments diverge from the column singly or singly and in pairs. In the gynoecium, ten carpel primordia initiate as two sets of five. The two sets (or whorls) of carpel primordia initiate alternately in the same "spatial whorl". Initiation within each set of carpel primordia is simultaneous. In most taxa, the second set of carpels is fertile and the first set is sterile. The sterile carpels may invaginate to varying degrees but do not form a locule with ovules. The bases of the sterile carpels may or may not contribute to forming the side of
the fertile locules. Even though the bases of the sterile carpels become indistinct in the five-locular ovary, styles and stigmas develop on each of the ten carpel primordia. Pollen is typically spherical, polyporate, and spiny; the exception is *Pavonia strictiflora* with smooth grains. The fruit type is a fleshy or dry schizocarp with various types of surface coverings. Floral nectaries are present at the inner bases of the sepals.

The aspects of floral ontogeny among Malvavisceae are sufficiently uniform to support retaining the tribe as such. They share many ontogenetic and morphological characters. I question, however, the inclusion of *Goethea* into the genus *Pavonia*. *Malvaviscus arboreus* shares more similar ontogenetic characteristics (including variable bractlet merosity, androecial teeth that are opposite the petals, and fertile carpels that are opposite or intermediate between opposite and alternate to petals) with *Pavonia bahamensis* and *Pavonia spinifex* than does *Pavonia strictiflora*. *P. strictiflora* also differs from the other *Pavonia* species and *Malvaviscus* with regard to bractlet and sepal color and function. *P. strictiflora* seems more closely allied with *Urena lobata*, with which it shares characteristics such as fixed bractlet merosity, androecial teeth positioned alternate with the petals, and the first set of carpels opposite the petals. Also, *Goethea* is unique in the family in having pollen without spines (Fryxell and Hashmi, 1971). This information would seem to argue against Fryxell's (1999) inclusion of *Goethea strictiflora* in *Pavonia*. Before definitive lines can be drawn between these genera or others, however, many more species of each genus needs to be examined to determine how much ontogenetic variation there is within a genus. *Pavonia* is a rather large, diverse genus and with the examination of more taxa, the differences I found in *P. strictiflora* may well fall within the diversity of
the genus. Based on the taxa studied so far, *Urena lobata* stands somewhat apart from the other members of the tribe by lacking bractlet and sepal ring meristems, by having simultaneous sepal initiation, having fused bractlets, and with the first set of carpels being fertile. *Malachra* is set apart by having floral bracts rather than bractlets.

In addition to verifying diagnostic features of the tribe and characterizing the tribe, ontogeny (revealed through the use of SEM) has been instrumental in clarifying the formation of unusual floral features such as the fused multistaminate androecium, the formation of ring meristems and common primordia, and the reduction of locule number in the gynoecium. Comparative floral ontogenetic studies can also be a powerful tool to elucidate similarities and differences among genera and species and to test tribal affinities.

**LITERATURE CITED**


INTRODUCTION

Hibisceae and Gossypieae are two of the five currently recognized tribes comprised in the plant family Malvaceae. Their taxa differ from the Malvavisceae and Malveae tribes in having capsular fruits rather than schizocarps. The tribe Decaschistieae also has capsular fruits; this tribe contains one genus that was until recently placed in Hibisceae (Fryxell 1968, 1975, 1988).

Delineation between the Hibisceae and Gossypieae and their placement in Malvaceae have been disputed. Early taxonomic treatments (Macout and Decaisne, 1876; Schumann, 1891; Edlin, 1935; Kearney, 1951; Hutchinson, 1967) placed members of Gossypieae in the Hibisceae tribe. Edlin (1935) moved the members from these tribes to the family Bombacaceae so that representatives of the Malvaceae contained only schizocarpous fruits. Kearney (1951) and Hutchinson (1967) retained the Hibisceae, including members of the Gossypieae, in Malvaceae. In 1968, Fryxell resurrected and redefined the Gossypieae, separating it from Hibisceae. Although Fryxell (1968) retained both these tribes in the Malvaceae, he noted that in some particulars the Hibisceae resembled the balance of the Malvaceae while the Gossypieae do not. He concluded that the Gossypieae do not belong in the Bombacaceae either, as suggested by Edlin (1935) and others, and that consideration should be given to elevating
in rank the group of genera in Gossypieae from tribe to family, distinct from either the Malvaceae or the Bombacaceae.

The Hibisceae Reichenb. emend. Alef. currently has 53 genera (Fryxell, 1968, 1975, 1997). The species (_Hibiscus lasiocarpos_, _Kosteletzkya virginica_, _Radyera farragei_, and _Abelmoschus manihot_) chosen for this research have not been in question as far as their placement in the Hibisceae. _Hibiscus_ is a large genus consisting of approximately 200 species native to the Americas, Africa, Asia, and Australia. The genus includes many ornamentals and some fiber crops. _Kosteletzkya_ consists of 17 species that occur in the New and Old World. _Abelmoschus_ is an Asiatic genus of about 15 species, many which have been introduced elsewhere in cultivation. Among the more well known in this genus is _A. esculentus_, which provides an edible fruit known in English as okra (Fryxell, 1988, 1997). At one time, _Abelmoschus_ was considered a section of the genus _Hibiscus_, but has since been accepted as a separate genus (Kearney, 1951; Fryxell and Hashmi, 1971; Fryxell, 1997). The genus _Radyera_ consists of two species, one from South Africa and one from Australia (Fryxell and Hashmi, 1971). _Radyera_ was formerly submerged in _Hibiscus_ by Hutchinson (1967) and others, but was segregated out by Fryxell and Hashmi (1971).

The Gossypieae Alefeld is comprised of eight genera (Fryxell 1968, 1979). Three species have been selected for this research: _Gossypium hirsutum_, _Thespesia populnea_, and _Cienfuegosia ulmifolia_. _Gossypium_ is a genus with about 50 species of tropical and subtropical distribution; many of them are found in Africa, the Middle East, Australia, Mexico and South America (Fryxell, 1988, 1997). Several species of _Gossypium_ have been cultivated and grown for cotton fibers, cotton-seed oil, and protein-rich seed meal (Hutchinson,
The genus Thespesia is a genus with 17 species located in New Guinea, Asia, Africa, the West Indies, and rarely in Mexico. The genus Cienfuegosia contains 25 to 26 species found in the southernmost United States, Central and South America, the West Indies, Africa, and the Arabian peninsula (Fryxell, 1968, 1988, 1997).

Members of the Malvaceae are tropical to temperate trees, shrubs, or herbs. The flowers are typically solitary or fasciculate in leaf axils or grouped in inflorescences. They are usually pentamerous, polysymmetric, and bisexual with an involucel or involucre, a monadelphous androecium, and a superior gynoecium. Anthers are bisporangiate and monothecal. Fruits are schizocarps, capsules, or sometimes berries. Pollen is typically spheroidal and echinate (Fryxell, 1968, 1975, 1988; Cronquist, 1981).

The Hibisceae is distinguished from other Malvaceae tribes not by any single character but by a combination of characters. Features that in combination delineate the tribe are: capsular fruit with five mericarps, a one to one ratio of stigmas to mericarps, five free styles in the gynoecium, five teeth at the apex of the staminal column, absence of gossypol glands, and the absence of involucral nectaries (Fryxell, 1968, 1975,1988).

The Gossypieae is primarily separated from the rest of the family on the basis of embryo characteristics and the presence of gossypol glands (Fryxell, 1968, 1979). The gossypol glands are lysigenous pigment glands and are believed to be unique both structurally and biochemically to this tribe (Fryxell, 1979). Other characteristics that help to define the tribe are a capsular fruit with three to five mericarps, three to five connate stigmatic lobes in the gynoecium, five teeth at the apex of the staminal column, presence of involucral nectaries, and several pollen characteristics (Fryxell, 1968,1988).
One purpose of this project is to make a comprehensive study of floral ontogeny in the Hibisceae and Gossypieae using scanning electron microscopy (SEM). Previous studies that dealt with floral development of some of the members of these tribes have used light microscopy techniques. Payer (1857) looked at various stages of floral development in many malvaceous taxa. Saunders (1936) and Rao (1952) described the vascular system of several malvaceous taxa, van Heel (1966) examined the androecium of numerous malvaceous species, and Gore (1935) examined the inflorescences of cotton (*Gossypium*). SEM was used by Ault (1987) to look at floral development in *Hibiscus acetosella*, by Moncur (1981) to look at floral initiation in *Gossypium hirsutum* and *Hibiscus cannabinus*, and by Christensen (1986) to look at the pollen morphology. None of these studies, with the exception of Ault (1987), included a complete ontogenetic series to show floral development in a member of these two tribes.

Another purpose of this research is to add insight through a knowledge of development to the many unusual structural features in flowers of Hibisceae and Gossypieae. One such structural anomaly found in malvaceous flowers is the fused multistaminate androecium with an adnate corolla. Little is known about how the stamens and petals initiate in this family. Accounts of androecial development have been very general; no studies have shown a complete detailed ontogenetic series for development of each of the many sets of stamens. Previous literature (Payer, 1857; Gore, 1935; van Heel, 1966; Sattler, 1973, Moncur, 1981; Endress, 1981; Ault, 1987, and Ch. 2) is contradictory as to the possible presence of a petal-stamen ring meristem or of common petal-stamen primordia; therefore, members of the Hibisceae and Gossypieae need to be examined further. This study will try to determine the
detailed patterns of stamen proliferation and the nature of the association
between the petals and the androecium in representative members of these
two tribes.

Another developmental question is how the bisporangiate (unilocular)
condition arises in the stamens of this family. Attempts have been made by
Payer (1857), Saunders (1936), and van Heel (1966) to attribute the
development of these half anthers to the division of bilocular stamens.
According to my observations with the Malvavisceae (Ch. 2), the bisporangiate
condition does not correlate with the bifurcation of stamens. I found that in
members of the Malvavisceae, some of the stamen primordia do not bifurcate
and some bifurcate once, yet all of the anthers are typically bisporangiate. In
addition, the mature filaments may diverge singly, in pairs, or in more complex
patterns from the androecial column (van Heel, 1966). Even though all of the
taxa I examined in the Malvavisceae have at least some stamens resulting
from bifurcations of common primordia, not all of the taxa have some stamens
diverging in pairs. Therefore, other factors besides just bifurcation must be
involved in determining how the filaments diverge from the column (Ch. 2).
The androecia in flowers of the Hibisceae and Gossypieae need to be
examined to see how they compare with those of Malvavisceae and to
determine if the bisporangiate condition and the patterns of filament
divergence can be correlated with early initiation of stamen primordia.

The descriptions of carpel development for many of the genera in
Malvaceae vary as to whether they initiate as one discrete whorl, as two
whorls, or as randomly scattered carpels (Bates, 1968; van Heel, 1978). Gore
(1935) described the gynoecia in cotton flowers as "first evident as a zonal
meristem slightly raised at three to five definite points." Sattler (1973)
suggested the formation of a carpel "rim" in some taxa. Payer (1857) describes the initiation of independent carpel primordia in a whorl in some malvaceous taxa (Hibiscus, Abelmoschus, Malva, Sphaeralcea, and Pavonia) with fusion occurring later. In Kitaibelia and Malope, he describes a pentagonal gynoecium with proliferation of numerous carpels occurring from five common "humps". Ault (1987) describes initiation of five carpel primordia with subsequent development of a gynoecial tube in H. acutosella. In the Malvavisceae, I found that the carpels initiate as two sets (or whorls) of five in a single "spatial whorl" and that no ring meristem was involved (Ch. 2). One focus of this research is to clarify how carpels initiate in members of the Hibisceae and Gossypieae.

A final aspect of this paper is to characterize and compare the Hibisceae and Gossypieae using ontogenetic characters. This research is part of a larger study to characterize and compare the tribes of Malvaceae and to use ontogenetic characters as well as morphological characters to determine the phylogeny of the tribes and genera. Tribes of Malvaceae have changed in content over the years, depending on the researcher. Comparative floral development can elucidate systematic differences among taxa. The overall aim of this study is to use scanning electron microscopy to compare floral development in representative examples of the tribes of Malvaceae, to test the validity of current tribal assignments.

**MATERIALS AND METHODS**

Floral material of four taxa in the Hibisceae (Hibiscus lasiocarpos, Kosteletzky virginica, Radyera farragei, and Abelmoschus manihot) and of three taxa in the Gossypieae (Gossypium hirsutum, Thespesia populnea, and Cienfuegosia ulmifolia) was collected from various sources (Table 3.1).
TABLE 3.1. Sources of Hibisceae and Gossypieae plant material and voucher information for taxa examined in this floral study.

<table>
<thead>
<tr>
<th>Taxon</th>
<th>Voucher</th>
<th>Source, collector, and date</th>
</tr>
</thead>
<tbody>
<tr>
<td><strong>Hibisceae</strong></td>
<td></td>
<td></td>
</tr>
<tr>
<td><em>Abelmoschus manihot</em> (L.)</td>
<td>TSC-0071</td>
<td>Cultivated by P. Evans at Louisiana State University, East Baton Rouge Parish, LA, US, origin - USDA PI #497112, from Guinea, by T. Crozier, Nov., 1992</td>
</tr>
<tr>
<td><strong>Hibiscus lasiocarpos</strong></td>
<td>TSC-0011, 0024</td>
<td>Weeds from St. Tammany and East Baton Rouge Parishes, LA, US, by T. Crozier, June, 1992</td>
</tr>
<tr>
<td><strong>Radyera farragii</strong> (F.v.M.)</td>
<td>TSC-0054</td>
<td>From P. Fryxell's greenhouse at Texas A &amp; M University, College Station, TX, US, origin - South Australia, by T. Crozier, Aug., 1992</td>
</tr>
<tr>
<td><strong>Gossypieae</strong></td>
<td></td>
<td></td>
</tr>
<tr>
<td><em>Cienfuegosia ulmifolia</em></td>
<td>TSC-0056</td>
<td>From P. Fryxell's greenhouse at Texas A&amp;M University, College Station, TX, origin - Argentina, by T. Crozier, Aug., 1992</td>
</tr>
</tbody>
</table>
Herbarium vouchers were made and retained by the author. Floral buds of various developmental stages were collected and fixed in formalin-acetic acid-alcohol (FAA). Prior to dissection, buds were transferred through two to four changes of 95% ethanol, then dissected in 95% ethanol. Material was dehydrated in 100% ethanol and critical point dried in a Denton DCP-1 with liquid CO2. Specimens were mounted on aluminum stubs with Avery press-on Spot-O-Glue and sputter-coated with gold-palladium in an Edwards S-150 apparatus. Micrographs were taken using a Cambridge S-260 scanning electron microscope at 15 kV and spot size 6. Kodak Tri-X (TXT 4164) sheet film was used.

Some late stage floral characters were obtained by examination of herbarium vouchers and FAA-ethanol preserved material with various dissecting and light microscopes. In some instances, literature was used to verify and complete mature floral descriptions. Terminology pertaining to floral features found in members of the Malvaceae are defined in chapter 2.

RESULTS

Hibiscus lasiocarpos -- Organography -- The plants are shrubs with flowers solitary in the leaf axils or sometimes on short axillary branches. The pedicels are distinctly jointed. The involucel consists of 10 to 14 green, distinct, linear bractlets. The five-lobed calyx is green and usually slightly exceeds the bractlets in length. The large white or pink corolla is five-merous and spreads distally. Each petal base has a crimson or maroon blotch. The androecium is included and is antheriferous throughout. The gynoecium is terminated by five distinct stigmas. The capsules are enclosed by the calyx,
are oblong to ovoid, and taper to an erect beak (observations of collected material; Bates, 1965; Correll and Johnston, 1979; Fryxell, 1988).

**Initiation and early development of the involucel and calyx** -- The 10 to 14 involucellar bracts initiate in an apparently helical sequence from a low ring meristem on the periphery of the floral apex (Figs. 3.1, 3.2). The bractlet primordia quickly elongate and arch over the remaining floral apex (Fig. 3.2). Initially the pre-sepal apex is slightly convex (Figs. 3.1, 3.2), but after all the bractlets have initiated, a low ring meristem develops around the remaining floral apex (Fig. 3.3). On this ring meristem, the five sepals initiate simultaneously (Fig. 3.4). As the sepals enlarge, they are ontogenetically fused at the base (Figs. 3.5, 3.6) and arch inward to cover the remaining floral apex (Figs. 3.9, 3.10).

**Initiation and early development of the corolla and the androecium** -- The apex to the interior of the sepals is initially convex and pentagonal in outline (Fig. 3.4). As this pre-petal apex enlarges, a central depression develops so that a petal-stamen ring meristem is formed (Fig. 3.5). Next, the ring meristem develops five common petal-stamen mounded regions or sectors that are interior and alternate to the sepals (Fig. 3.6). As the ring meristem enlarges laterally and vertically and thus becomes more defined, the five common mounds or regions become less defined and five petal primordia initiate simultaneously on the lower peripheral flank of the ring meristem (Fig. 3.7). In other words, one petal initiates on the outer perimeter of each of the five barely-defined common petal-stamen regions; thus the remaining apical portion of each sectorial region is potential androecial tissue. This places the petals interior and alternate to the sepals (Fig. 3.7). After the petals have initiated, the two side-by-side common stamen primordia initiate on the upper
portion of each sectorial region of the ring meristem. Therefore, the ring meristem is divided apically into ten common stamen primordia or mounds, two of which are opposite and associated with each petal (Fig. 3.8). Five of these common stamen primordia are slightly taller and radially broader than the five alternating ones. At this stage, the calyx and the involucel form protective coverings for the bud (Figs. 3.9, 3.10), and the remaining floral apex in the center of the petal-stamen ring meristem is relatively flat; there is no sign of carpel initiation (Figs. 3.10, 3.11). As the petals broaden laterally and become blade-like, each of the ten common stamen primordia divide into radial rows of common stamen primordia (Figs. 3.12, 3.13). Since the most advanced common stamen primordia in these rows appear to be on the lower interior surface of the ring meristem and as one proceeds outward on the ring the primordia are smaller and less defined, this would indicate centrifugal division of the ten original primordia (Fig. 3.12). One of the paired rows of common stamen primordia (the leading row) in each of the five sectorial regions of the ring meristem starts more to the interior on the ring meristem than the other row (the lagging row). The five leading rows develop from the larger five of the ten original common primordia. A small area of the inner ring meristem remains in front of each of the lagging rows (Figs. 3.12, 3.14). This means that in each sector of the ring, the most interior-formed primordium does not have a complementary primordium beside it; rather, there is space (R in Fig. 3.12) left on the meristem. All subsequent common primordia in each sectorial region on the ring meristem initiate centrifugally in lateral pairs. With regard to the micrographs, labeling of each row of common stamen primordia begins with the number 1, for the most-interior and first-formed primordia, and progresses outward with each centrifugal initiation primordia. It should be
noted that at this stage in development, the carpel primordia have initiated (Figs. 3.12, 3.13). As the androecial ring meristem expands laterally and elongates vertically, paired common stamen primordia continue to initiate centrifugally in each sectorial region on the ring meristem until numerous common primordia are formed (Figs. 3.15, 3.16). It is not uncommon to have as many as eight common stamen primordia in each leading row and seven in each lagging row; stamen numbers vary within the species. Each of the common primordia will laterally broaden to become elliptic in shape (the newer formed primordia begin as rather broad mounds and continue to widen) (Figs. 3.15, 3.16), then become peanut-shaped (Figs. 3.17, 3.18), and finally bifurcate into two stamen primordia (Fig. 3.18). Crowding near the apex of the ring meristem (now elongating into a column) causes some of the bifurcations to occur in an oblique direction (Figs. 3.16 - 3.18). Concurrently with the broadening of the common stamen primordia, the five remaining spaces (R) on the ring meristem elongate in an upward direction and initially form five sterile teeth which alternate with the first five common primordia at the top of the androecial column (T in Figs. 3.17, 3.18). Further elongation of the column produces a five-lobed tube which extends beyond the divergence of the stamen from the androecium (Fig. 3.21). The distal portion of each stamen primordium enlarges and an indentation forms between the two microsporangial regions. This differentiation of the bisporangiate anthers on the column appears to be nearly simultaneous, with the younger stamens on the lower portion of the column lagging only slightly behind the older stamens in development (Figs. 3.19 - 3.21). At least early in development, the filaments appear to diverge from the column in lateral (sometimes oblique or vertical) pairs (Fig. 3.22).
Petal elongation is retarded until after all the stamen primordia are formed (Figs. 3.17 - 3.18). As the petals elongate, they form a contort corolla (Figs. 3.18 - 3.20). The petal bases are ontogenetically fused to the base of the androecium (Figs. 3.15 - 3.19, 3.21).

**Initiation and early development of the gynoecium** -- Carpel primordia are initiated concurrently with the proliferation of the ten common stamen primordia into radial rows of common stamen primordia (Fig. 3.12). The five carpel primordia are initiated simultaneously in one spatial whorl and are interior and alternate to the petals and to the common petal-stamen regions (Figs. 3.12 - 3.14, 3.23). As the carpel primordia enlarge, a small dimple appears on the adaxial surface of each (Fig. 3.24). Further invagination produces a locular cavity in each carpel (Figs. 3.25, 3.26). As the gynoecium further develops, the carpel bases fuse so completely that it is difficult to distinguish one carpel base from another when viewing the external wall of the ovary. (Figs. 3.27 - 3.29). The carpel tips grow upward and inward towards the center of the flower (Figs. 3.27 - 3.28) and partially fuse to form a stylar column (Fig. 3.29). Apical residuum remains in the center of the floral apex and is not initially incorporated into the gynoecial primordia (Figs. 3.23 - 3.27). In each locule, numerous ovules are initiated from bottom to top along the inner margins of the enrolled carpel walls (Figs. 3.28, 3.29). Ovule development occurs before the styles are exserted beyond the androecial column (Figs. 3.30, 3.31). Stigma differentiation, apparent by the apical portion of each style broadening and developing stigmatic surface texture (Fig. 3.30), does not occur until after the gynoecium has elongated beyond the androecium.
Midstage and mature reproductive characters -- The involucellar bracts remain distinct and immediately subtend the calyx. In the mature calyx, sepals are fused about half their length. Nectarial trichomes are found on the inner side of the sepal bases. The calyx lobes equal or more commonly exceed the length of the involucel. The petals remain distinct from each other but are ontogenetically fused to the base of the androecium. They lack auricles, are double to triple the length of the calyx, and spread distally to form an open showy flower.

Filaments diverge along the entire length of the androecial column in the mature flower. The filaments diverge singly or in lateral, oblique, or vertical pairs; sometimes two pairs of filaments are very closely associated. The filaments diverge radially from the column, but the long filaments of some stamens bend around so that all of the anthers are presented on one side of the column. This positions the anthers on the upper side of the androecial column in the horizontally (or nearly so) positioned flowers. The apex of the androecial column bends upward in conjunction with the gynoecial column. Anther dehiscence is longitudinal. The five sterile teeth are on a small tube at the apex of the androecial column.

The styles of the gynoecium are fused most of their length, only separating at the very upper portion of the column after it surpasses the androecium. In the nearly horizontally positioned flower, the tip of the gynoecial column bends upward and presents five capitate stigmas. The gynoecial column is half or less the length of the corolla, but is quite visible inside the flared corolla. The ovary, which starts off relatively smooth (Fig. 3.29), becomes distinctly five-lobed. Each of these five main lobes becomes bilobed in accordance with the two bulging vertical rows of ovules inside
Figs. 3.1 - 3.6. *Hibiscus lasiocarpos*, initiation of bractlets, sepals, petal-stamen ring meristem, and common petal-stamen primordia. Bars = 100 μm. 3.1. Low bractlet ring meristem (R) around the periphery of the floral apex (A). Some bractlets have initiated in helical sequence (order of initiation shown with numbers, with 1 being the first-initiated primordium). 3.2. Bractlet primordia (Bt) arch over the remaining slightly convex floral apex. Young trichomes have initiated on the bractlets. 3.3. Sepal ring meristem. Bractlets have been removed. 3.4. Five sepal primordia (S) have initiated simultaneously on the ring meristem. The remaining floral apex is slightly convex and five-sided. 3.5. A petal-stamen ring meristem is distinguished by a central depression in floral apex. The sepals are fused at the base. 3.6. Sepals have enlarged and partially arch over the floral apex. Five mounded sectorial regions (m, only two labeled) are present on the petal-stamen ring in positions interior and alternate to the sepals.
Figs. 3.7 - 3.12. *Hibiscus lasiocarpos*, petal-stamen ring meristem and initiation of petals and stamens. Bars = 100 μm. 3.7. Common petal-stamen ring meristem with five barely defined mounded regions. Five petal primordia (P, only one labeled), one in each sectorial region, have initiated simultaneously on the outer flanks of the ring meristem and five barely defined common stamen primordia (St, only one labeled) occupy the apex of the ring meristem. Petals alternate with the sepals. 3.8. Upper portion of ring meristem with ten barely defined common stamen primordia (St, only two labeled), two in each sectorial region on the ring meristem. This places two stamen primordia opposite and interior to each petal. 3.9. The calyx has arched over and protects the floral apex. Note fusion between the sepal bases. Different types of trichomes have developed on the sepal surfaces. 3.10. Vertical dissection of bud to illustrate well defined petal-stamen ring meristem. Stage represented is after petal initiation, when there are ten common stamen primordia on the apex of the ring meristem. Note that the remaining floral apex is relatively flat. 3.11. Ten well defined common stamen primordia and five petal primordia are on the ring meristem. 3.12. Proliferation of common stamen primordia in a centrifugal direction with ten radial rows of common stamen primordia initiated in place of the ten original common stamen primordia (Proliferation sequence of one sectorial region is shown with numbers). A small area of the inner ring meristem (R, only one labeled) remains in front of each of the five lagging rows of common stamen primordia. Petal primordia have broadened laterally and have become more blade-like. Simultaneous initiation of five carpel primordia (C, only two labeled) interior to and alternate to the petals and to the common petal-stamen regions.
Figs. 3.13 - 3.18. *Hibiscus lasiocarpos*, stamen proliferation. Bars = 200 μm. 3.13. Proliferation of common stamen primordia in a centrifugal direction with ten radial rows of common stamen primordia (sequence of initiation in one sectorial region is shown with numbers). Five carpel primordia are barely visible interior to the androecium. 3.14. Older common stamen primordia are more pronounced and have broadened laterally to an elliptic shape. Younger common stamen primordia have initiated in a centrifugal direction on the expanded ring meristem. Five spaces still remain on the ring meristem (R, one labeled). Carpel primordia are present. 3.15. The androecial ring meristem has elongated vertically. More common stamen primordia have initiated centrifugally on the ring meristem. The common stamen primordia have broadened laterally. The petals are adnate to the androecium. 3.16. Stamen proliferation has continued in a centrifugal direction. Most of the common stamen primordia are laterally broad; some near the apex of the column are obliquely broad. 3.17. Further initiation of stamens. Sterile teeth (T, only two labeled) are present at the top of the androecial column. The older common stamen primordia near the top of the column are peanut-shaped and some have bifurcated (shared numbers with ' label the bifurcated primordia). 3.18. The common stamen primordia have bifurcated laterally to produce four radial rows of stamen primordia opposite each petal (i.e. per region). Near the apex only five pairs of stamens are present; these alternate with the sterile teeth. Note that the last-formed stamens at the base of the column no longer lag behind the upper stamens in development. Petals have elongated and their margins overlap slightly.
Figs. 3.19 - 3.22. *Hibiscus lasiocarpos*, differentiation of stamens and elongation of petals. Bars = 500 μm. 3.19. The distal portions of the stamen primordia have enlarged and the earlier-formed primordia have indentations between the microsporangial regions. The contort corolla is adnate to the androecium. Sterile teeth are opposite half of each petal. 3.20. Further differentiation of anthers on the androecial column and elongation of petals in the contort corolla. 3.21. Sterile teeth tube has elongated and the five gynoecial styles (sl, only one labeled) have elongated inside the androecial tube. Petal scars show adnation to the androecium. 3.22. Early stage of stamen differentiation with filaments (f) diverging from the androecial column in pairs. Anthers = (a).
Figs. 3.23 - 3.28. *Hibiscus lasiocarpos*, initiation and early development of the gynoecium. Bars = 100 μm. 3.23. Five carpels have initiated simultaneously in one whorl in positions alternate with the petals and to the common petal-stamen regions. An apical residuum (r) remains interior to the gynoecium. 3.24. Gynoecial whorl with adaxial dimples (two shown at arrows) in the carpel primordia. 3.25. Locular cavity (one shown at arrow) formation in all five carpels. 3.26. Partial androecium (Ad) and gynoecium with further development of the five carpel locules. Carpels are positioned alternate with and interior to the sterile teeth. 3.27. Partial gynoecium with apical residuum. Carpels tips have elongated in an upward and inward direction. 3.28. Gynoecium with one carpel partially dissected to reveal development of ovules (O, only two labeled). The ovules are initiated from bottom to top on the inwardly-folded margins of the carpels.
Figs. 3.29 - 3.31. *Hibiscus lasiocarpos*, gynoecial development. Bars = 200 μm in 3.29 and 3.31, = 2 mm in 3.30. **3.29.** Young gynoecial column with fusion of the ovary (V) and along the bases of the five young styles (si, only one labeled). One carpel is partially dissected to reveal immature ovules. **3.30.** Longitudinal section of young floral bud with sepals and bractlets removed. Styles are emergent beyond the androecial column. Ovules are present in a locule (at arrow). Petal bases are adnate to the base of the androecium. **3.31.** Partially-developed ovules (enlargement of Fig. 3.30).

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each locule. Numerous ovules develop in each locule. No twisting occurs along the length of the androecial or gynoecial columns. Floral symmetry, with regard to the perianth, is actinomorphic. The pollen grains are spheroidal, echinate (spiny), and polyporate.

*Kosteletzkya virginica* -- **Organography** -- The plants are herbs with flowers in terminal, often leafy racemes or panicles. The pedicels are jointed. The involucel consist of six to ten green, distinct, linear bractlets. The five-lobed calyx is green and exceeds the bractlets in length. The five-merous corolla distally spreads and is lavender, pink, or white. The androecium is included and is nearly antheriferous throughout. The capsules are five-angled and depressed (observations of collected material; Radford, Ahles, and Bell, 1987; Correll and Johnston, 1979; Fryxell, 1988).

**Initiation and early development of the involucel and calyx** -- The involucellar bracts initiate in helical sequence (Figs. 3.32, 3.33) on a poorly defined ring meristem around the periphery of the floral apex (Fig. 3.32). As the bractlet primordia enlarge, they arch over the remaining floral apex (Fig. 3.33). The pre-sepal apex is initially convex (Fig. 3.34); then a low ring meristem develops around the periphery (Fig. 3.35). On this ring meristem the sepals initiate in simultaneous order (Fig. 3.35). As the sepals enlarge, they arch over the remaining floral apex and are basally fused (Figs. 3.37, 3.38).

**Initiation and early development of the corolla and the androecium** -- The apex to the interior of the sepals is initially convex and pentagonal in outline (Fig. 3.36). Next, a petal-stamen ring meristem develops and on this ring five common petal-stamen mounded regions initiate interior and alternate to the sepals (Fig. 3.37). The ring meristem then becomes distinctly pentagonal in outline, with the common mounds at the corners of the pentagon.
The five petal primordia initiate simultaneously on the outer flank of the ring meristem, one on the lower abaxial surface of each common petal-stamen mound (Fig. 3.40). The petals are interior and alternate with the sepals. Just after or concurrent with petal initiation, five common stamen primordia become distinct on the upper surface of the ring meristem, one in each sectorial region (Fig. 3.41). These common stamen primordia are irregular in shape, with one lateral side higher and wider than the other (Fig. 3.41), and this feature becomes accentuated as the primordia enlarge (Figs 3.42, 3.43). On each of the common stamen primordia, three smaller common stamen primordia initiate nearly simultaneously, so that the ring meristem now bears 15 common stamen primordia (Fig. 3.44). Therefore, each sectorial region consists of a lagging stamen row (which at this stage consist of only one primordium) and a leading row (which consists of two radially aligned primordia, with the larger and more defined primordia innermost on the ring meristem). Five small spaces remain on the ring meristem interior to the lagging stamen rows (R in Fig. 3.44). Next, each of the 15 common primordia broaden and becomes elliptic in shape (Fig. 3.45). The ten common primordia innermost on the ring meristem broaden in a radial plane or centripetal direction and take on the peanut shape before the other common primordia. The other common primordia broaden in an oblique manner, something in between a radial and a lateral direction (Figs. 3.45, 3.46). Ten more primordia initiate centrifugally on the ring meristem, two laterally oriented in front of each petal (Fig. 3.46). The 15 peanut-shaped common primordia bifurcate to make two stamen primordia each (Figs. 3.47 - 3.48). It is unclear whether the ten outermost primordia on the ring meristem (which become the lowest on the vertical androecial column) each develop
into one stamen, bifurcate to make two stamens each, or even of all of them develop (Figs. 3.49, 3.57). Anther differentiation occurs at the same time the androecium is elongating into a column (Figs. 3.48 - 3.50). The five spaces that remain on the inner portion of the ring meristem elongate to form five sterile teeth at the apex of the androecial column (Figs. 3.48 - 3.50, 3.57, 3.59). The petals are adnate to the base of the androecium (Fig. 3.47). Petal elongation is delayed until the anthers begin to differentiate (Figs. 3.48, 3.50). As the petals elongate and broaden, they overlap to form a contort corolla (Figs. 3.48, 3.50).

Initiation and early development of the gynoecium -- Carpels are initiated concurrent with bifurcation of common stamen primordia (Fig. 3.51). The five carpels initiate simultaneously in a single whorl in positions interior and alternate to the petals. At the time the androecium is elongating into a column, each carpel primordium develops an invagination on the adaxial surface (Fig. 3.52). Further development of the gynoecium produces basal fusion of the members and a deep locular crevice in each carpel (Fig. 3.53). The tips of the carpels grow upward and inward (Fig. 3.54) and form a fused stylar column (Figs. 3.55, 3.59). The bases of the five carpels fuse into an ovary (Figs. 3.54, 3.55) with five locules that each produce one ovule (Fig. 3.56). Development of both the ovules (Fig. 3.55) and the styles (Figs. 3.58, 3.59) begins before the styles surpass the androecial column.

Midstage and mature reproductive characters -- The bractlets remain distinct and immediately subtend the calyx. Nectary trichomes develop on the inner side of the sepal bases (Fig. 3.58). The mature sepals are longer than the bractlets and are fused 1/4 to 1/3 their length. The petals are distinct from
Figs. 3.32 - 3.38. *Kosteletzkya virginica*, initiation of bractlets, sepals, petal-stamen ring meristem, and common petal-stamen mounds. Bars = 100 μm. 3.32. Initiation of bractlets on periphery of floral apex. Bractlet initiation appears to be helical or some variation of helical (possible sequence shown with numbers). Note that this flower has been damaged; the primordia labeled 3 and 5 have been pushed towards the center of the bud. A low bractlet ring meristem is barely defined by a depression between the outer rim of the floral apex and the convex center of the floral apex. 3.33. Bractlet primordia arch over the remaining floral apex. Possible helical sequence of initiation of bractlets, based on size of primordia, is shown with numbers. 3.34. Pre-sepal floral apex is slightly convex. Most of the bractlets have been removed. 3.35. Low sepal ring meristem precedes initiation of sepal primordia. 3.36. Five sepal primordia have initiated simultaneously. The remaining floral apex is pentagonal in outline and slightly convex. 3.37. Common petal-stamen ring meristem with five mounded sectorial regions (m, only 1 labeled). The depression in the center of the apex helps to define the ring meristem. 3.38. Sepals are fused basally and arched apically over the remaining floral apex.
Figs. 3.39 - 3.44. *Kosteletzkya virginica*, initiation of petals and common stamen primordia. Bars = 100 μm. 3.39. The petal-stamen ring meristem is pentagonal in outline. Five mounds are present on the ring meristem. 3.40. Petals have initiated on the outer abaxial portion of the common petal-stamen mounds. The five petal primordia have initiated simultaneously on the outer flank of the ring meristem in positions alternate to the sepals (only one sectorial region labeled). 3.41. Petal primordia have become more distinct and five common stamen mounds have initiated simultaneously on the upper surface of the ring meristem, one in each sectorial region. These mounds are irregular in shape. The remaining floral apex is flat. 3.42. The five common stamen primordia have become more defined. 3.43. Further development of the five common stamen primordia and petals. The remaining floral apex is flat. 3.44. Three common stamen primordia have initiated on each of the five original common stamen primordia. Primordia in one sectorial region are labeled with numbers to show the leading row (with 2 primordia) and the lagging row (with one primordium). Small spaces (R) remain on the inner rim of the ring meristem interior to the lagging stamen rows.
Figs. 3.45 - 3.50. *Kosteletzkya virginica*, proliferation of stamens and development of petals. Bars = 200 μm. 3.45. The 15 common stamen primordia have elongated centripetally or obliquely. The innermost primordia are slightly broader and more peanut shaped than the outer common stamen primordia on the ring meristem. 3.46. All of the 15 early common stamen primordia are peanut shaped. Ten more common primordia, two in each region, have initiated centrifugally on the ring meristem. 3.47. The 15 early common primordia have bifurcated. Petals have laterally broadened. Petals are adnate to the androecium. 3.48. Further differentiation of the stamen primordia. Bifurcated stamen primordia are labeled with ('). Five small spaces remain on the upper inner surface of the ring meristem. Petals have overlapped to form a contort corolla. 3.49. Development of anthers and sterile teeth. The androecial ring meristem has elongated vertically into a column. Incompletely developed stamens are present at the base of the column (at arrows). 3.50. Contort corolla surrounding androecial column. Five sterile teeth are at the apex of the androecium.
Figs. 3.51 - 3.56. *Kosteletzkya virginica*, carpel initiation and development. Bars = 100 μm in 3.51 and 3.52, = 200 μm in 3.53 and 3.54, = 500 μm in 3.55 and 3.56. 3.51. Partial androecium and gynoecium. Simultaneously initiated carpels are in a single whorl. 3.52. Gynoecium and partial androecium and corolla. The carpel primordia have small adaxial invaginations (one at arrow). 3.53. Young flower bud with androecium and corolla (P) removed to expose gynoecium. The five carpels (only 1 labeled) are basally fused and have developed adaxial crevices. 3.54. Gynoecium with apical portions of carpels elongated into young styles. The carpels are basally fused. 3.55. Young stylar column with partially dissected ovary. 3.56. Partially dissected young ovary base reveals five locular cavities with one ovule in each. The ovary is five-sided, with each corner of the pentagon on a radius with a locule and its ovule. The lower surface of each corner of the pentagon has a small indentation (two shown at arrows).
Figs. 3.57 - 3.62. *Kosteletzkya virginica*, mid and late stage floral development. Bars = 500 µm in 3.57 and 3.60, = 2 mm in 3.58, 3.59, and 3.62, = 50 µm in 3.61. 3.57. Androecial column with five sterile teeth at the apex (only 1 labeled). Most of the column is surrounded by anthers except at the base where a few stamen primordia are underdeveloped (two at arrows). Petals are adnate to the androecium. 3.58. Later stage of floral development with young stigmas (sm) emerged beyond the androecial column. Part of the contort corolla has been removed. A trichome nectary (N) is present on the inner sepal bases. 3.59. Longitudinal section of a young floral bud. Styles with capitate stigmas are exerted beyond the androecium. Filaments appear to diverge singly from the androecial column. Sterile teeth are at the apex of the androecium. 3.60. Ovary and base of stylar column. The corners of the earlier formed pentagonal ovary have each developed a longitudinal groove and have bulged outward in accordance with the enlarged underlying ovule (fertilization may have occurred). 3.61. Nearly mature pollen grain. The pollen is spheroidal and covered with spines. 3.62. Immature fruit with partial calyx. The capsule is five angled and covered with trichomes.
each other, lack auricles, and are adnate to the androecial base. At maturity, they distally spread to form an open flower.

Most filaments diverge singly along the entire length of the androecial column (Fig. 3.59). At maturity, they diverge radially around the column, but some bend to present most of the anthers to one side of the column; this positions most of the anthers on the upper side of the column in the nearly horizontally positioned flowers. In addition, the distal portion of the androecial and gynoecial columns bend to position the column tips vertically in the flowers. The five sterile teeth are on a small tube at the apex of the androecial column. Anther dehiscence is longitudinal.

The styles of the gynoecium are fused most of their length, only separating at the very upper portion of the column after it surpasses the androecium. The height of the gynoecium in the open flower may equal, slightly exceed, or be slightly less than petal height. The stigmas are capitate. The ovary, which starts off relatively circular (Fig. 3.54), becomes five-sided (Fig. 3.56). Each corner of the pentagon is on a radius with a locule and its ovule (Fig. 3.56). With subsequent development of the ovary, each of these corners develops a longitudinal groove along with a bulge around the underlying ovule (Fig. 3.60).

No twisting occurs in the androecial or gynoecial columns. Floral symmetry, with regard to the perianth, is actinomorphic. The pollen grains are spheroidal, echinate, and polyporate (Fig. 3.61). The capsular fruit is wider than tall, five-angled, and covered with trichomes (Fig. 3.62). In the mature fruit, bractlets and sepals persist and the sepals have the same radial orientation as the angles of the fruit.
Abelmoschus manihot -- Organography -- The plants are subshrubs with flowers solitary in leaf axils. The pedicels are not jointed. The involucel consists of four to six green, lanceolate to ovate bractlets. The green sepals are connate. The tubular calyx splits asymmetrically and falls off with the corolla at anthesis. The large five-merous corolla is yellow with a red center. The androecium is included. The styles are fused into a column that is terminated by sessile capitate stigmas. The capsules are elongate and apically acuminate and each contain many seeds (observations of collected material; Fryxell, 1988). This particular collection of A. manihot is unusual in that it has ten carpels per flower and thus a ten-locular fruit; typically this genus has a five-carpellate flower and a five-locular fruit.

Initiation and early development of the involucel and calyx -- The bractlets (typically five in this type) appear to initiate in helical sequence on the periphery of the floral apex (Fig. 3.63). It is not known if a ring meristem precedes bractlet initiation. The pre-sepal apex is at first slightly convex (Fig. 3.63), then a low ring meristem develops to the interior of the bractlet primordia (Fig. 3.64). Concurrent with this ring meristem becoming more pronounced, five sepal primordia are simultaneously initiated on its upper surface (Figs. 3.65, 3.66). Early vertical elongation at the base of this sepal ring produces a tubular calyx with five apical lobes (Figs. 3.67 - 3.69). The sepals arch over and protect the remaining floral apex (Figs. 3.68, 3.69).

Initiation and early development of the corolla and the androecium -- As in the other taxa sampled from this tribe, a pronounced petal-stamen ring meristem forms (Fig. 3.70). In this taxon, however, the five common petal-stamen mounds are barely (if at all) defined (Figs. 3.66, 3.67) during early ring meristem formation and are not apparent later in development as the ring
meristem broadens and elongates (Fig. 3.70). Simultaneous initiation of five petal primordia on the outer rim of the ring meristem coincides with simultaneous initiation of ten common stamen primordia on the inner rim of the ring meristem (Fig. 3.71). The petal position appears to be alternate with the sepals (Fig. 3.78). As in the other taxa, the common stamen primordia are paired on the same radius as each petal primordium (Fig. 3.71). As the petal primordia broaden laterally, the ten common stamen primordia divide into radial rows of common stamen primordia (Figs. 3.72, 3.73). As in *H. lasiocarpos*, there are five leading and five alternate lagging rows of centrifugally initiated common stamen primordia. It follows then that there is a small space remaining on the ring meristem in front of each of the lagging rows of common stamen primordia (R in Figs. 3.72, 3.73). As the androecial column expands laterally and elongates vertically, stamen proliferation continues in a centrifugal direction (Figs. 3.74, 3.75) until there are as many as eight common stamen primordia in each of the leading rows and seven in each of the lagging rows (Fig. 3.76); the numbers vary from flower to flower. Before all of the common stamen primordia have initiated, the older primordia broaden laterally and become elliptic in shape; the primordia closest to the apex are crowded and broaden in an oblique direction (Fig. 3.75). The last-formed primordia near the base of the expanded androecium begin as rather broad protuberances and continue to widen (Figs. 3.75, 3.76). Each of these common stamen primordia progresses from elliptic-shaped to peanut-shaped, then bifurcates into two stamen primordia (Fig. 3.76). Differentiation of the anthers proceeds from top to bottom of the column, with the younger stamens at the base of the column lagging only slightly behind the older stamens (Figs. 3.77 - 3.79). Concurrent with bifurcation of the common stamen primordia, the
five spaces in front of the lagging stamen rows on the ring meristem enlarge (Fig. 3.76); and at the time of anther differentiation, these mounded areas project upward to form sterile teeth (Figs. 3.77 -3.79). Very early in development, the stamen filaments appear to diverge singly or in pairs (Fig. 3.84) but, with further elongation of the column, they appear to diverge singly (Fig. 3.80). As with H. lasiocarpos, petal elongation is delayed (Figs. 3.74 - 3.76) until all of the stamen primordia have initiated. As the petals elongate, they form a contort corolla (Fig. 3.78) with the petal bases adnate to the androecium (Figs. 3.76, 3.78).

Initiation and early development of the gynoecium  -- Carpel initiation occurs sometime after the stamen primordia begin to proliferate centrifugally. At this time, I have insufficient material to obtain the earliest stages of carpel initiation. The earliest stages of the gynoecium that I was able to obtain have ten carpels (Fig. 3.81) that are in one fused spatial whorl. I was unable to determine if all ten of these carpels initiate at the same time. Five of the carpels are less broad and slightly shorter than the other five alternating carpels (Figs. 3.81 - 3.83). As in the other taxa, an apical residuum is interior to the gynoecial whorl (Fig. 3.83). All ten of the carpels form small invaginations (Fig. 3.81), then crevices (Figs. 3.82, 3.83), and then fertile locules (Figs. 3.84 - 3.86). The apical portion of each carpel primordium elongates vertically and inwardly (Fig. 3.84) to form a stylar column. As the members of the gynoecium proceed through stylar differentiation, half of the young styles are slightly shorter than the other five (Figs. 3.84, 3.87). Ovule development occurs before the styles are exserted beyond the androecial column (Fig. 3.84). As in H. lasiocarpos, the ovules develop from bottom to top along the inwardly folded carpel margins (Figs. 3.84, 3.85).
Figs. 3.63 - 3.68. *Abelmoschus manihot*, initiation of bractlets, sepals, petal-stamen ring meristem, and common petal-stamen primordia. Bars = 100 μm. 3.63. Bractlet primordia with size difference indicating possible helical initiation (order of initiation shown with numbers). The pre-sepal apex is slightly convex. 3.64. Pre-sepal apex with the development of a low ring meristem around the periphery. 3.65. A more pronounced sepal ring meristem with five sepal primordia. The pre-petal apex is relatively flat. 3.66. The sepal primordia are ontogenetically fused. The pre-petal apex has a barely visible depression in the center and five low mounds interior and alternate to the sepal lobes (m, only two labeled). 3.67. Five sepal lobes at the apex of the calyx tube. The remaining pre-petal apex has a large invagination in the center and five low mounds that are alternate to the sepals. 3.68. The calyx has vertically elongated and arches over the remaining floral apex.
Figs. 3.69 - 3.74. *Abelmoschus manihot*, initiation of petals and stamen proliferation. Bars = 200 μm, except in 3.69 = 1 mm. 3.69. The calyx (S, only one sepal lobe labeled) forms a five-lobed tube arching over and protecting the remaining floral apex. No fusion has occurred among the bractlets. 3.70. Petal-stamen ring meristem is delineated by a deep central depression in the floral apex. The petal-stamen ring meristem is smooth; there are no (or at least not any easily discernible) common petal-stamen mounds. 3.71. Early stage of petal initiation on the outer surface of the ring meristem. The five petals (only 1 labeled) have initiated simultaneously. The upper surface of the ring meristem is divided into ten common stamen primordia (St, only two labeled). 3.72. There are five leading and five lagging rows of common stamen primordia (only one sectorial region has been labeled). The five leading rows have divided centrifugally. The petal primordia have broadened laterally. There is no sign of carpel initiation on the remaining floral apex. 3.73. Further development of petal primordia and more pronounced furrowing between the ten radial rows of common stamen primordia. No carpels are visible on the remaining floral apex. 3.74. Centrifugal initiation of common stamen primordia. Petal primordia have broadened and become blade-like.
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Figs. 3.81 - 3.86. *Abelmoschus manihot*, development of the gynoecium. Bars = 200 μm in 3.81 - 3.83 and 3.85, = 1 mm in 3.84, = 500 μm in 3.86. 

**3.81.** Partially dissected androecium and corolla. Gynoecium with ten carpel primordia in one spatial whorl. Each carpel primordia has a small adaxial invagination (one shown at arrow). Five carpel primordia are less broad and slightly shorter than the other five alternating carpel primordia. 

**3.82.** Gynoecium with adaxial crevices (two shown at arrows) in all ten carpel primordia. 

**3.83.** Gynoecium with deep crevices in all ten carpels. Five of the carpels are still broader and taller than the other five. All of the carpels have started to elongate apically. An apical residuum is interior to the gynoecial whorl. 

**3.84.** Partial androecium. Two of the staminal filaments (f) appear to diverge together. The apical portion of each carpel primordia is elongated vertically and inwardly. Dissection of the young ovary to show ovule formation in each carpel. 

**3.85.** Enlargement of dissected ovary in Fig. 3.84. Ovules initiate on the inner surfaces of the two enrolled margins of each carpel. The ovules develop from bottom to top along the carpel margins. 

**3.86.** Development of numerous ovules in each locule.

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Figs. 3.87 - 3.90. *Abelmoschus manihot*, midstage development. Bars = 1 mm in 3.87, 2 mm in 3.88, = 500 μm in 3.89, = 50 μm in 3.90. 3.87. Longitudinal section of androecium and gynoecium. The styles have elongated to different heights and are fused into a column that is terminated by immature capitate stigmas. The stigmas have begun differentiation before they have emerged beyond the androecium. Sterile teeth are present at the top of the androecial column. 3.88. Young ovary and partial styal column. Longitudinal suture lines develop on the outer surface of each locule. 3.89. Sessile capitate stigmas on young pistil. Note the height difference in the styles. 3.90. Spheroidal and echinate pollen grain.
Immature stigmas are apparent before the gynoecial column emerges beyond the androecium (Fig. 3.87).

**Midstage reproductive characters** -- The involucellar bracts remain distinct and immediately subtend the calyx (Fig. 3.78). While still in the closed bud stage, the sepals are fused. The petals are distinct, fused to the base of the androecium (Fig. 3.78), and later form an open showy flower.

Five sterile teeth emerge at the top of the androecial column (Figs. 3.77, 3.78, 3.87). At midstage in development the stamen filaments appear to diverge singly from the androecial column (Fig. 3.80). The styles are fused their entire length and are terminated by sessile capitate stigmas; i.e. the column is terminated by an irregularly ten-lobed stigma (Fig. 3.89). Difference in height of the styles and stigmas can still be seen late in floral development (Fig. 3.89). The surface of the ovary develops longitudinal sutures over each locule (Fig. 3.88). Numerous ovules develop in each locule (Fig. 3.86). The pollen grains are spheroidal, echinate (Fig. 3.90), and polyporate.

**Radyera farragel** -- **Organography** -- The plants are erect herbs with flowers in dense clusters at the end of stout axillary peduncles. The short pedicels are not jointed. The involucel consist of ten (9 to 11) green bractlets that are basally fused and apically geniculate. The five-lobed calyx is green and slightly longer than the involucel. The five-merous corolla is lavender or purple and spreads distally. The androecium is included and is antheriferous throughout, except at the base. The gynoecium is terminated by a single five-lobed capitate stigma. The fruit is a capsule (observations of collected material; Fryxell and Hashmi, 1971).

**Initiation and early development of the involucel and calyx** -- Each flower initiates in the axil of a small leaf with two stipules. The leaf initially
appears as a large primordium flanked by two smaller ones, the stipules (Figs. 3.91, 3.92). As each leaf primordium enlarges, it becomes unequally three-lobed (Figs. 3.91 - 3.93). The bractlets in this species have an unusual order of initiation. The bractlets do not initiate as individual primordia, but rather as common primordia that subsequently become lobed and divide. The bractlets occur in one whorl on the periphery of the floral apex (Figs. 3.92, 3.94). A ring meristem is not present prior to bractlet initiation (Fig. 3.92). The first step involves the initiation of three large common bractlet primordia in helical sequence on the periphery of the floral apex, with the last-formed primordium generally adjacent to the subtending leaf (Figs. 3.91 -3.93). Next, each of these large common primordia becomes unequally three-lobed, similar to the leaf primordia. As the lobing becomes more defined, each common primordium divides, becoming a group of three bractlet primordia with each group consisting of a large primordium flanked by two smaller ones (Figs 3.92 - 3.96). The number of bractlets in later stage flowers is usually ten. The extra bractlet may result from splitting of one of the nine primordia (two of the bractlets are usually very close together and have a greater amount of fusion than their counterparts) or by extra primordia subsequently initiating on the space sometimes left on the bractlet rim (Fig. 3.94); however, I have seen no evidence of the latter. In the early stages of bractlet development, they grow in a vertical direction rather than arching over the apex, and thus do not appear to function as protection for the ensuing sepal whorl (Fig. 3.96). Basal fusion of the bractlets begins concurrent with the formation of the petal-stamen ring meristem (Figs. 3.98, 3.100).

The pre-sepal apex is circular in outline and slightly convex (Figs. 3.91 - 3.93). A sepal ring meristem is not present. The five sepal primordia initiate in
a helical sequence, with the first sepal primordium initiating opposite to the largest bractlet primordium (Figs. 3.94 - 3.96). The sepal primordia quickly equalize in size (Fig. 3.97) and arch over the remaining floral apex (Figs. 3.99, 3.101).

Initiation and early development of the corolla and the androecium -- The pre-petal apex is initially relatively flat and pentagonal in outline (Fig. 3.96). As the sepal primordia equalize in size, the remaining floral apex becomes slightly convex (Fig. 3.97) and develops a central depression characteristic of a ring meristem (Figs. 3.98 - 3.100). On this ring meristem, five common petal-stamen mounded regions develop alternate to the sepals (Figs. 3.98, 3.99). As in Hibiscus lasiocarpos, on each of these mounded regions a petal primordium initiates on the outer perimeter and two common stamen primordia initiate on the raised portion (Figs. 3.100, 3.101). It appears that petal initiation precedes or occurs at the same time as initiation of the first ten common stamen primordia (Fig. 3.100). The order of initiation within these whorls is simultaneous. Five of the common stamen primordia enlarge precociously, especially broadening radially earlier than the five smaller alternating common primordia (Fig. 3.102). These five larger common stamen primordia proliferate centrifugally sooner than the five smaller primordia and thus form the leading stamen rows (Figs. 3.103, 3.104). In this species, the designation of leading rows is based only on the premise of early proliferation; the leading rows do not appear to be located more to the interior on the ring meristem than the lagging rows. There is no space left on the ring meristem interior to the lagging stamen rows. As the androecial column expands laterally and elongates vertically, centrifugal proliferation continues until each row contains approximately eight common stamen primordia (Figs.
Before all of the common stamen primordia have initiated centrifugally, the older primordia nearest the center of the column broaden obliquely (Fig. 3.105) and become elliptic (Fig. 3.106), then peanut-shaped (Figs. 3.106, 3.107). All of the centrifugally initiated common stamen primordia, except possibly the last-formed set of primordia at the base (outer edge) of the column, bifurcate in an oblique direction to form two stamen primordia each (Fig. 3.108). Differentiation of the anthers proceeds from top to bottom of the column, with the younger stamens at the base of the column lagging only slightly behind the older stamens (Fig. 3.108). The portion of the ring meristem interior to the stamen primordia enlarges as the androecial column elongates and broadens. This ring of tissue does not have any distinctive lobes, but it is pentagonal in outline with the corners of the pentagon in radius with the petals (Figs. 3.106, 3.107). As elongation of this tissue continues, a sterile-tube with a variable number of lobes will develop at the top of the androecium. As with H. lasiocarpos, petal elongation is delayed (Figs. 3.103 - 3.105) until all of the stamen primordia have initiated. As the petals elongate, they form a contorted corolla (Figs. 3.107, 3.108) with petal bases adnate to the androecium (Fig. 3.108).

Initiation and early development of the gynoecium -- Carpel initiation occurs after the first ten common stamen primordia have initiated (Figs. 3.103, 3.104). The five carpel primordia initiate simultaneously in positions interior to the petal-stamen ring meristem and on the same radii as the petals (Figs. 3.103, 3.104, 3.109). All of the carpel primordia form small adaxial invaginations (Fig. 3.110), then crevices (Fig. 3.111), and then fertile locules (Figs. 3.112 - 3.114). The apical portion of each carpel primordium elongates vertically and inwardly (Fig. 3.111) to form a stylar column (Figs. 3.112, 3.113).
Figs. 3.91 - 3.96. *Radyera farragei*, floral shoot and initiation of bractlets and sepals. Bars = 200 μm in 3.91, 3.92, and 3.94, = 100 μm in 3.93, 3.95, and 3.96. 3.91. Oblique view of inflorescence. The lower left flower is in the axil of a three-lobed leaf primordium (L) with stipular primordia (sp). In the center of the shoot is a younger unlobed leaf primordium with stipular primordia. Flowers at the top center of the micrograph have bractlet primordia (Bt). 3.92. Polar view of inflorescence in Fig. 3.91. The most central flower has three common bractlet primordia that arose in a helical sequence (order of initiation shown with numbers). On the left flower, each of the three bractlet primordia has become three-lobed or three-parted. The order of initiation for these divided bractlets is shown with (') numbers, with the members of the first-formed group all numbered 1'. 3.93. Three groups of bractlet primordia on a floral apex. The three helically-initiated common bractlet primordia have each become three-parted, with a large bractlet primordium in the center and two smaller bractlet primordia on each side. The flower is in the axil of a three-lobed leaf primordium and a pair of stipule primordia. The pre-sepal apex is slightly convex and circular in outline. 3.94. Whorl of helically-initiated groups of bractlet primordia on the periphery of the floral apex. Note the space remaining in the whorl between the second and third bractlet groups. The first sepal primordia has initiated (at arrow). 3.95. Helical initiation of first three sepal primordia (order shown with numbers). 3.96. Five sepal primordia. The pre-petal apex is pentagonal in outline and relatively flat.
Figs. 3.97 - 3.102. *Radyera farragei*, initiation of petal and common stamen primordia. Bars = 200 μm. 3.97. The five sepal primordia are nearly equal in size. The pre-petal apex is slightly convex. 3.98. A central depression has developed in the pre-petal apex. 3.99. Pre-petal apex with more defined central depression indicating a ring meristem. Five common petal-stamen mounds are on the ring meristem in positions alternate to the sepals. 3.100. The five common petal-stamen mounds are less evident. A radial indentation has developed in the middle of each common petal-stamen mound (sectorial region), initiating two common stamen primordia. On the outer flank each sectorial region a petal primordium has initiated. The bractlets are basally fused. 3.101. Ten common stamen primordia are present on the upper portion of the ring meristem and five petal primordia are present on the periphery (only one sectorial region labeled). The sepals have elongated and arch over the remaining floral apex. 3.102. Five of the common stamen primordia have broadened radially. These will form the leading rows of stamen primordia. The floral apex in the center of the petal-stamen ring meristem is relatively flat; no carpel primordia are present.
Figs. 3.103 - 3.108. *Radyera farragei*, development of petals and proliferation of stamens. Bars = 200 µm in 3.103 - 3.105, = 500 µm in 3.106 - 3.108. 3.103. Androecium with centrifugally initiated common stamen primordia (shown with numbers for one region). Five barely-defined carpel primordia are present interior to the petal-stamen ring meristem. The carpel primordia are opposite the petals. 3.104. Androecium with ten radial rows of common stamen primordia. The stamen primordia in each row have initiated centrifugally (shown with numbers in one region). Each carpel primordium has a small invagination on the adaxial surface. 3.105. The older common stamen primordia have broadened obliquely. The petal primordia are becoming more blade-like. The gynoecium consists of five carpel primordia. 3.106. The older common primordia near the top of the androecial column have bifurcated in an oblique direction. The meristematic tissue (R) at the top of the androecial column has enlarged; this tissue will eventually form a tube with sterile teeth. 3.107. Androecial column with peanut-shaped common stamen primordia. The petals overlap in the corolla. One of the carpels is visible; it has a large locular cavity (at arrow). 3.108. The bases of the petals are adnate to the androecium. Differentiation of the anthers is most advanced at the top of the androecium.
Figs. 3.109 - 3.114. *Radyera farragei*, initiation and development of carpels. Bars = 200 μm in 3.109, 3.111, and 3.112a, = 100 μm in 3.110, = 500 μm in 3.113a and 3.114a, b figures are 4X magnification of corresponding a figures. 3.109. Lateral view of partially dissected petal-stamen ring meristem. Five carpel primordia have initiated to the interior of the ring meristem (only four are visible from this perspective, only one is labeled). 3.110. Polar view of a gynoecium and part of an androecium. Each carpel primordium has an adaxial invagination. 3.111. Gynoecium and partial androecial column. The carpels have developed locular crevices. 3.112a Gynoecium with the tips of the carpel primordia elongated inward and upward. Ovule development has started inside the young carpels. 3.112b. Enlargement showing ovule development from bottom to top along the inwardly folded carpel margins. 3.113a. Gynoecium with development of the ovary and the base of the young stylar column. 3.113b. Enlargement of a locular cavity with six incompletely developed ovules. 3.114a. Polar view of ovary base. Placentation is axile. Many ovules develop in each locule. 3.114b. Enlargement of ovules.
Figs. 3.115 - 3.118. *Radyera farragei*, mid and late stage floral development. Bars = 250 μm in 3.115 and 3.118, = 50 μm in 3.116, = 2 mm in 3.117. 3.115. Apical portion of nearly mature gynoecium. The styles are fused their entire length. The stigma is five-lobed and capitate. 3.116. Pollen grains in an anther prior to anthesis. The pollen grains are oblate to suboblate, zonicolporate, and spiny. 3.117. Longitudinal section of a young flower bud prior to opening. The bractlets and sepals are apically geniculate. The sepals are closed over the corolla and androecial column. 3.118. Young androecial column. The filaments diverge in pairs.
Ovules develop from bottom to top along the inwardly folded carpel margins (Figs. 3.112, 3.113). Many ovules form in each carpel locule (Figs. 3.113, 3.114).

Midstage and mature reproductive characters -- The involucellar bracts are fused more than 2/3 of their length and immediately subtend the calyx. Both the bractlets and the sepals are apically geniculate (Fig. 3.117). The calyx slightly surpasses the involucel in length. The petals are distinct from each other and basally fused to the androecium. They lack auricles, are approximately triple the length of the calyx, and spread distally to form an open showy flower.

The stamen filaments diverge along most of the length of the androecial column. The filaments diverge radially from the column and mostly in pairs (Figs. 3.117, 3.118); a few appear to diverge singly. Although there are teeth at the apex of the androecial column, the number, size, and spacing of teeth is variable.

The styles of the gynoecium are fused their entire length and each bears a capitate stigma; this might also be described as a column terminated by a five-lobed capitate stigma (Fig. 3.115). The gynoecium is approximately half the length of the corolla. No twisting occurs along the length of the androecial or gynoecial columns. Floral symmetry is actinomorphic. The pollen grains are oblate to suboblate, zonicolporate, and spiny (Fig. 3.116).

Gossypium hirsutum -- Organography -- The plants are shrubs with flowers axillary or in sympodial inflorescences. The pedicels are not jointed. The involucel consist of three large, green, distinct, foliaceous bractlets. The five-lobed calyx is green and is shorter than the bractlets. The large cream-colored or pale yellow corolla is five-merous and spreads distally. Each petal
may have (or lack) a dark spot at the base. The androecium is included and antheriferous throughout. The gynoecium is terminated by a fused stylar column and three to five decurrent stigmatic lobes. The capsules are ovoid or subglobose in shape (observations of collected material; Fryxell, 1988).

Initiation and early development of the involucel and calyx -- The three bractlet primordia initiate in a helical sequence on the periphery of the floral apex (Figs. 3.119 - 3.121). A ring meristem is not involved in bractlet initiation. Each bractlet primordium becomes apically lobed soon after initiation (Figs. 3.121, 3.122); apical lobing also occurs to the subtending leaf primordia (Fig. 3.119). The bractlet primordia elongate and arch over the remaining floral apex (Fig. 3.122). The pre-sepal apex is convex and triangular in outline corresponding to the trimerous involucel (Fig. 3.123). The sepal primordia appear to initiate in helical sequence, with the first three initiated concurrently with a sepal ring meristem (Figs. 3.124, 3.125) and the last two primordia initiated after the ring meristem has become more pronounced (Fig. 3.126). As the sepals enlarge, they are ontogenetically fused at the base and form a calyx tube with five unequal-size lobes (Fig. 3.127, 3.128). The calyx tube arches over the remaining floral apex (Fig. 3.128).

Initiation and early development of the corolla and the androecium -- The apex to the interior of the sepals progresses in shape from convex and round in outline (Figs. 3.124, 3.125) to relatively flat and pentagonal in outline (Figs. 3.126, 3.127). The corners of the pentagonal apex become slightly raised, but distinct common petal-stamen mounds do not form (Fig. 3.127). As the pre-petal apex enlarges, a shallow central depression develops so that a low petal-stamen ring meristem is formed (Fig. 3.129). On the periphery of the ring meristem, five petal primordia initiate simultaneously (Fig. 3.129).
The petals are positioned alternate to the sepals. Concurrently with petal initiation, five common stamen mounds initiate simultaneously on the raised surface (interior to the petals) of the ring meristem (Fig. 3.129). As the central depression deepens and the ring meristem becomes more defined, the five common stamen primordia each develop a radial groove (Fig. 3.130). Similar to Hibiscus lasiocarpos, ten radial rows of common stamen primordia develop on the ring meristem, two opposite to subopposite to the petal in each sectorial region (Figs. 3.131, 3.132). In each radial row, the common stamen primordia initiate in a centrifugal direction (Figs. 3.132, 3.133). In the case of this particular collection of Gossypium hirsutum, many aberrations occur in the paired radial rows of common stamen primordia. Often, one very broad primordium initiates instead of paired lateral primordia (Figs. 3.132, 3.134). In some flowers, three lateral primordia initiate in a sectorial region rather than two (Fig. 3.133). There does not appear to be a set of leading and lagging common stamen rows in this taxon; none of the rows originate more interior on the ring meristem or proliferate centrifugally earlier than the other rows. There are no spaces remaining to the interior of the stamen rows on the upper surface of the ring meristem (Fig. 3.132). At the time the stamen are proliferating centrifugally, the petals broaden and become blade-like (Figs. 3.133, 3.134). They are adnate to the androecium (Fig. 3.132). As the petals begin to overlap to form a contorted corolla, the innermost common stamen primordia broaden in an oblique or lateral direction (Figs. 3.133, 3.134). Six common stamen primordia may initiate in each radial row; numbers vary (Fig. 3.135). Each common stamen primordium broadens, becomes elliptic, then peanut-shaped, and finally bifurcates into two stamen primordia (Figs. 3.135 - 3.136). At the time anther differentiation occurs, five sterile teeth elongate and
emerge from the top of the androecial column (Figs. 3.137, 3.138, 3.142). The filaments often diverge in pairs from the column (Fig. 3.142). Petal elongation is retarded until after all the common stamen primordia have initiated (Figs. 3.134, 3.135).

Initiation and early development of the gynoecium -- A carpel ring meristem (Fig. 3.139) initiates after the ten common stamen primordia begin to proliferate centrifugally. On this ring meristem three to five carpel primordia initiate in a simultaneous order (Fig. 3.140). All of the carpel primordia invaginate (Fig. 3.141), form crevices (Fig. 3.142), and then fertile locules. The carpel bases are ontogenetically fused and form a syncarpous ovary (Fig. 3.142). The carpel tips grow upward and inward towards the center of the flower (Fig. 3.142). An apical residuum remains in the center of the floral apex and is not initially incorporated into the gynoecial primordia.

Mature reproductive characters -- The involucellar bracts remain distinct and immediately subtend the calyx. In the mature calyx, the sepals are fused about three-fourths the length. The involucel greatly exceeds the calyx in length. The petals remain distinct from each other, lack auricles, are about five times longer than the sepals, and are adnate to the base of the androecium. The petals spread distally to form an open showy flower.

The filaments diverge singly or in pairs. Sometimes, two filaments are fused almost to the point of anther attachment. The stamen filaments diverge radially from the column. The small, triangular-shaped sterile teeth are much shorter than the stamen filaments which extend beyond the top of the fused androecial column.

The gynoecium is exserted beyond the fused portion of the androecium, but it is about equal to or slightly exceeds the total height of the filaments and
Figs. 3.119 - 3.122. *Gossypium hirsutum*, floral shoot and initiation of bractlets. Bars = 500 μm in 3.119, = 100 μm in 3.120 - 3.122. 3.119. Polar view of floral shoot. The flower to the left with the bractlet primordia removed has a sepal ring meristem. In the center of the micrograph, a flower with one bractlet primordium is in the axil of a lobed-leaf primordium with two stipular primordia. The flowers to the right present different stages of bractlet initiation. 3.120. Three bractlet primordia have initiated in helical sequence on the floral apex (the sequence of bractlet initiation is shown with numbers). No bractlet ring meristem is present. 3.121. The older two bractlet primordia (numbers 1 and 2) are lobed apically. The pre-sepal apex is convex. 3.122. The members of the involucel have elongated, have become multi-lobed, and arch over the remaining apex. A sepal ring meristem has initiated.
Figs. 3.123 - 3.128. *Gossypium hirsutum*, sepal initiation and development. Bars = 200 μm. 3.123. The pre-sepal apex is triangular in outline and convex. The three bractlets have been removed. 3.124. Sepal ring meristem with three sepal primordia. The sepals initiate helically (order shown with numbers). The pre-petal apex is convex. 3.125. The sepal ring meristem is more pronounced. The pre-petal apex is convex and circular in outline. 3.126. The sepal ring meristem has elongated and broadened so that the sepal whorl is more circular than triangular in outline. All five sepal primordia have initiated. The pre-petal apex is flatter and more pentagonal in outline. 3.127. The calyx is ontogenetically fused at the base and has five unequal-sized lobes. The pre-petal apex is relatively flat and pentagonal in outline, with the corners of the pentagon slightly raised. 3.128. The calyx tube has arched over the remaining floral apex. The lobes of the calyx tube are unequal in size. An androecial ring meristem (Ad) with common stamen primordia and a gynoecial ring meristem (C) has initiated to the interior of the calyx.
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Figs. 3.135 - 3.138. *Gossypium hirsutum*, development of petals and stamens. Bars = 250 µm in 3.135 and 3.136, = 500 µm in 3.137, = 1 mm in 3.138. 3.135. The androecial column and the petals have elongated. The petals are adnate to the androecium and have overlapped to form a contorted corolla. The upper common stamen primordia have bifurcated, while others on the column are peanut-shaped or elliptic. 3.136. Individual stamen primordia have developed except at the column base, where some common stamen primordia have not bifurcated yet. 3.137. Anther differentiation has started. Five sterile teeth have elongated at the top of the androecial column (only one labeled). 3.138. The anthers and the sterile teeth are more developed. Some of the anthers are shaped irregularly.
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anthers that extend beyond the apex of the androecial tube. The styles of the gynoecium are fused their entire length. The decurrent stigmatic lobes extend down about half the length of the stylar column. Inside each locule many ovules develop on the inwardly folded carpel margins (not illustrated).

No twisting occurs along the length of the androecial or gynoecial columns. Floral symmetry is actinomorphic. The pollen is spheroidal, colporate, and echinate. The capsular fruits are taller than wide and apically taper to a blunt point. The bractlets and sepals persist in the fruit (not illustrated).

*Thespesia populnea* -- **Organography** -- The plants are small trees with flowers solitary in the leaf axils. The pedicels are not jointed. The involucel consists of three green, distinct bractlets that fall off before the flower reaches maturity. The sepals are fused into a calyx cup. The large yellow corolla is five-merous and spreads distally. Each petal base has a maroon spot. The androecium is included and is antheriferous throughout. The gynoecium is terminated by a single style with five decurrent stigma lobes. The capsules are oblate, leathery, and indehiscent (observations of collected material; Fryxell, 1988).

*Initiation and early development of the involucel and calyx* -- The three bractlets initiate in helical sequence on the floral apex (Fig. 3.143). A ring meristem is not present in the bractlet whorl (Fig. 3.143). Even though all of the bractlets are positioned on the stout receptacle, not all of the bractlets are inserted at the same vertical level on the receptacle (Figs. 3.146, 3.149). As the bractlets enlarge, they spread distally and do not enclose and protect the inner floral organs. In fact, the bractlets remain relatively small and narrow. The pre-sepal apex is slightly convex. The sepals initiate in helical sequence
A low meristematic ring develops in the sepal whorl after initiation of the first sepal primordium (Figs. 3.145, 3.146). As the sepals enlarge, they are ontogenetically fused at the base (Fig. 3.148). The sepals form a tube with unequal-sized lobes that arch over the remaining floral apex (Figs. 3.148, 3.149), and then completely fuse to form a protective dome over the inner developing floral organs.

Initiation and early development of the corolla and the androecium --

The convex apex to the interior of the sepals develops a slight central depression (Fig. 3.150). Therefore, it is assumed that a ring meristem initiates prior to the petals and stamens. Five petal primordia and five common stamen primordia initiate on this ring meristem. It is unclear whether the petals or the stamens initiate first in this taxon. Based on equal size of the early primordia, the order of initiation of the petal whorl and the whorl of five common stamen primordia is presumed to be simultaneous (Fig. 3.151). Petal position is alternate to the sepals. The five common stamen primordia are positioned subalternate to the petals (Fig. 3.151). Each of the five common stamen primordia or regions partitions laterally into three common stamen primordia (Fig. 3.152). The three primordia in each sectorial region initiate with the central primordium more interior on the ring meristem than the other two; thus, forming a v-pattern of primordia (Figs. 3.152, 3.153).

As the androecial ring meristem expands laterally and elongates vertically, initiation of common stamen primordia continues in a centrifugal direction. Unlike the previously described taxa in this paper which basically initiate ten radial rows of common stamen primordia, *Thespesia populnea* tends to have a variable number of radial rows of common primordia. Instead of the common stamen primordia in each sectorial region initiating centrifugally
in lateral pairs, they initiate in lateral or oblique triplets or quads along part of
the column length (Figs. 3.154, 3.155), then eventually switch to lateral pairs
at the base of the column that bears the last-initiated organs (Fig. 3.156).
Therefore, at the midlevel of the column there can be as many as 20 irregular
rows of common stamen primordia, but at the base there are usually ten rows.
Each of the common stamen primordia broadens laterally and becomes elliptic
(Fig. 3.155), then peanut-shaped (Fig. 3.156), and then bifurcates into two
stamen primordia (Fig. 3.157). The last-formed common primordia at base of
the column are the last to bifurcate (Figs. 3.156, 3.157). Five lobes develop
on the inner surface of the ring meristem, one in each sectorial region (Fig.
3.155). As the ring meristem elongates, these five lobes elongate and
broaden to form five sterile teeth at the apex of the column (Figs. 3.156 -
3.159). Differentiation of the anthers and filaments proceeds from the top of
the column to the bottom (Fig. 3.158). All of the filaments appear to diverge in
lateral or oblique pairs (Fig. 3.158). Petal elongation does not appear to be
delayed as much as in the previous taxa; the petals enlarge and form a contort
corolla before all of the common stamen primordia have initiated (Figs. 3.153,
3.154). The petal bases are ontogenetically fused to the base of the
androecium.

Initiation and early development of the gynoecium -- The carpel
primordia initiate at the same time as the first 15 common stamen primordia
(Figs. 3.152, 3.160). A very low carpel ring meristem may be present at the
time (not before) carpel primordia initiate (Figs. 3.152, 3.160). The five carpel
primordia are initiated simultaneously in one spatial whorl and are opposite the
petals (Figs. 3.152, 3.153, 3.161). The adaxial surface of each carpel
primordium develops an indentation (Fig. 3.162), then an invagination
(Fig. 3.163), then a locular cavity. As the gynoecium enlarges, the carpel bases fuse into a syncarpous ovary and the apical portion of each carpel elongates to form a stylar column (Figs. 3.164, 3.166). An apical residuum remains interior to the young gynoecium. Ovule development occurs before the styles surpass the androecial column. Several ovules develop in each locule (Fig. 3.165). Swelling of the stigmatic region at the top of the styal column is apparent before the gynoecium has surpassed the level of the teeth at the top of the androecium (Fig. 3.167).

Midstage and mature reproductive characters -- In a young flower, the three bractlets are usually not all inserted at the same level on the receptacle. The bractlets fall off before the flower reaches maturity. In the immature buds, the sepals and petals are noticeably very thick (Fig. 3.167). The sepals fuse their entire length to form a calyx cup. The petals remain distinct from each other but are adnate to the base of the androecium (Fig. 3.167). The petals lack auricles, are generally four time longer than the sepals, and spread distally to form an open showy flower.

Stamen filaments diverge radially along the entire length of the androecial column in the mature flower. The filaments diverge in pairs, and sometimes two filaments are fused together almost to the point of anther attachment. The sterile teeth at the top of the column divide or split so that there appear to be between five and 15 irregularly spaced teeth. These teeth are long and linear like stamen filaments. The anthers dehisce by longitudinal slits.

The styles of the gynoecium are fused their entire length and the column is terminated by five decurrent stigma lobes. The gynoecium exceeds the androecium in height and is about half the length of the corolla.
Figs. 3.143 - 3.149. *Thespesia populnea*, bractlet and sepal initiation and development. Bars = 100 µm in 3.143 - 3.147, = 200 µm in 3.148 and 3.149. **3.143.** Helical initiation of first two bractlet primordia on the floral apex (the sequence of initiation is shown with numbers). **3.144.** Young flower with two of the three bractlets removed. The first sepal primordium has initiated and there is no sign of a sepal ring meristem. **3.145.** Two bractlets have been removed and one has been bent away from the apex. The two sepal primordia have initiated and a barely defined ring of meristematic tissue has developed in the sepal whorl. The pre-petal apex is convex. **3.146.** The sepal ring meristem is more defined. The pre-petal apex is convex. The bractlet scars are asymmetrical, with the base of each blade-like bractlet primordium having one edge slightly wider than the other edge. Not all of the bractlets are inserted at the same vertical level on the receptacle. **3.147.** All five sepal primordia have initiated, helical sequence of initiation is shown with numbers (the largest primordium has been removed). **3.148.** The sepals are ontogenetically fused at the base and are unequal in size. Most of the larger peltate trichomes have been removed. **3.149.** The calyx tube has unequal-sized lobes. The sepals are arched over the remaining floral apex. The pedicel is very stout and is covered in trichomes.
Figs. 3.150 - 3.155. *Thespesia populnea*, initiation of petal-stamen ring meristem, petals, and common stamens. Bars = 200 μm. 3.150. Pre-petal apex with central depression (at arrow). Two sepals have been removed. 3.151. Ring meristem with five petal primordia and five common stamen primordia or regions. The five common stamen primordia are positioned alternate to the petal primordia. 3.152. Three common stamen primordia have initiated on the upper adaxial surface of each of the five common stamen primordia regions. The central primordium (numbered 1) in each sectorial region is more interior on the ring meristem that the two flanking primordia (labeled 2). Five carpel primordia have initiated in positions alternate with the stamen regions and in radial line with the petals. 3.153. The stamen ring meristem has broadened and more common stamen primordia have initiated in a centrifugal pattern. Five carpel primordia are present. The petal margins have begun to overlap. 3.154. Ring meristem with centrifugally initiated common stamen primordia. The stamen primordia in each sectorial region are not in discrete paired radial rows. The petals have elongated and form a contort corolla. The carpels have adaxial invaginations. 3.155. The ring meristem has broadened and elongated. The youngest common stamen primordia are initiating centrifugally in four irregular radial rows (shown with arrows). Five small sterile teeth are present on the interior rim of the ring meristem. Notice that the five stamen regions are alternate rather than in a radial row with the petals.
Figs. 3.156 - 3.159. *Thespesia populnea*, stamen proliferation. Bars = 500 μm. **3.156.** Androecial column. The older common stamen primordia at the top of the column have become peanut-shaped, while common stamen primordia lower on the column are elliptic. The youngest common stamen primordia at the base of the column have initiated in centrifugal pairs. Five sterile teeth project upward at the apex of the androecial tube. **3.157.** The older common stamen primordia at the top of the androecial column have bifurcated. **3.158.** Young androecial column with some of the stamen removed. The filaments diverge in lateral or oblique pairs. Differentiation of the anthers and filaments has taken place in all except the last-formed primordia at the base of the column (at arrow). **3.159.** The sterile teeth at the top of the androecial column have elongated and become more linear. The tips of the styles are visible inside of the androecial column.

3.160. Simultaneous initiation of five carpel primordia. A very low carpel ring meristem is indicated by the central depression in the center of the apex and the slightly raised ring of tissue where the carpels have started to initiate.

3.161. Five carpel primordia in a single whorl. 3.162. Partial androecium and gynoecium. Each carpel primordium has a small indentation on the adaxial surface. 3.163. Each carpel primordium has an adaxial invagination. 3.164. The carpel bases have fused and the apical portion of each carpel has elongated upward and inward. 3.165. Partially dissected ovary. Several ovules have developed in each locule (two locules are visible at arrows).
Figs. 3.166 - 3.168. *Thespesia populnea*, midstage floral development and pollen. Bars = 2 mm in 3.166 and 3.167, = 50 μm in 3.168. 3.166. Young gynoecial column with fused styles. 3.167. Longitudinal section of young flower. The apical portions of the styles have broadened. The petals are adnate the androecium. The bases of the petals are very thick (as are the sepals). 3.168. Pollen grains.
No twisting occurs along the length of the androecial or gynoecial columns. Floral symmetry is actinomorphic. The pollen is spheroidal, spiny and colporate (Fig. 3.168). The capsules are wider than tall and have relatively large seeds.

**Cienfuegosia ulmifolia -- Organography --** The plants are herbs with flowers solitary in leaf axils. The pedicels are not jointed. The involucre is suppressed and not apparent in the mature flower. The calyx is green and five-lobed. The corolla is five-merous and spreads distally. The petals are yellow with a basal maroon spot. The androecium is included and is antheriferous throughout. The gynoecium is terminated by a single style with three capitate stigma lobes. The capsule is ovoid and has three locules (observations of collected material; Fryxell, 1967).

**Initiation and early development of the involucre and calyx --** Three bractlets initiate on the periphery of the floral apex in an apparently helical sequence (Figs. 3.169 - 3.171). No ring meristem is involved in bractlet initiation (Fig. 3.169). After all three bractlet primordia have initiated, the first sepal primordium initiates on the remaining convex floral apex (Figs. 3.169 - 3.171). Sepal initiation proceeds in a helical sequence and no ring meristem is involved (Figs. 3.172, 3.173). The bractlet primordia, although initiated, fail to enlarge and develop further (Figs. 3.172, 3.173) and they are not apparent by the time the petals have initiated (Fig. 3.174). The pedicels of the young floral bud become noticeably thickened (Fig. 3.174).

**Initiation and early development of the corolla and the androecium --** The apex to the interior of the sepals is initially slightly convex and pentagonal in outline (Fig. 3.173). A ring meristem forms with five common petal-stamen mounds or sectorial regions (Fig. 3.175). Concurrently or nearly so, ten
common stamen primordia initiate on the apex of the ring meristem and five petal primordia initiate on the outer peripheral flank. Thus each of the common petal-stamen mounds gives rise to one petal primordium and two laterally oriented common stamen primordia (Fig. 3.176). The order of initiation within the petal whorl and among the ten common stamen primordia is simultaneous. The petals are positioned alternate to the sepals (Fig. 3.174). With enlargement and broadening of the ring meristem, the ten common stamen primordia become broadened radially (Fig. 3.177). With further enlargement of the ring meristem, each of these ten common stamen primordia initiates a row of common stamen primordia centrifugally (Fig. 3.178). There appears to be a leading row and a lagging row of common stamen primordia in each sectorial region. Each row generally consists of five or six common stamen primordia (Figs. 3.178, 3.180). Each of these common stamen primordia broadens laterally or obliquely and becomes elliptic in shape, then becomes peanut-shaped, and finally bifurcates into two stamen primordia (Fig. 3.178). There appears to be some elongation at the base of each common stamen primordium prior to apical bifurcation (Fig. 3.181). The process of bifurcation occurs first in the earliest-formed common stamen primordia at the apex of the column and proceeds basipetally on the column (Figs. 3.178, 3.181). Five small sterile teeth initiate at the apex of the column (T in Figs. 3.178, 3.179). When differentiation of the stamens occurs, the filaments of each bifurcated stamen pair are partially fused (Figs. 3.179, 3.180). Petal elongation is retarded until after all the common stamen primordia have initiated. As the petals elongate, they form a contorted corolla (Fig. 3.178). The petal bases are fused ontogenetically to the base of the androecium (Fig. 3.180).
Figs. 3.169 - 3.174. *Cienfuegosia ulmifolia*, bractlet and sepal initiation. Bars = 100 \( \mu m \) except in 3.174 = 200 \( \mu m \). 3.169 - 3.171. Different views of a floral apex with three bractlet primordia. In the polar view, slight differences in size of the bractlets indicates that the order of initiation is probably helical (sequence of initiation shown with numbers). One sepal primordium has initiated on the convex apex. 3.172. Helical initiation of sepal primordia (sequence of initiation shown with numbers). No sepal ring meristem is present. 3.173. Five sepal primordia are present. The pre-petal apex is slightly convex and pentagonal in outline. 3.174. Floral shoot. The oldest flower on the right has had the sepals removed. The sepal scars are alternate with the petal primordia. On this older flower, the bractlets are no longer present and the pedicel is swollen.
Figs. 3.175 - 3.180. *Cienfuegosia ulmifolia*, initiation and development of petals and stamens. Bars = 100 µm in 3.175 - 3.178, = 1 mm in 3.179 and 3.180. 3.175. Five common petal-stamen mounds or regions have initiated on a petal-stamen ring meristem. 3.176. Five petal primordia have simultaneously initiated on the ring meristem, one on the abaxial portion of each common petal-stamen mound. On the raised portion of the ring meristem, ten common stamen primordia have initiated, two per sectorial region. 3.177. The petal primordia have become more defined and the ring meristem has broadened and elongated. The gynoecium has not initiated. 3.178. Androecium with ten radial rows of common stamen primordia. The oldest common stamen primordia at the top of the column have bifurcated, the common primordia in the middle of the column are peanut-shaped, and the youngest common primordia at the base of the column are elliptic. The petals have elongated, are growing marginally, and overlap at their margins. Five sterile teeth have initiated at the top of the androecial column. 3.179. Androecium, partly cut away. The filaments diverge in basally fused pairs. Sterile teeth are presented at the apex of the androecial column. The gynoecium consist of a young ovary and a single fused stylar column with three apical lobes. 3.180. Filaments diverge in basally fused pairs. Sterile teeth are at the apex of the androecial tube. The stylar column with three stigma lobes has surpassed the androecium. The petals are adnate to the androecium.
Figs. 3.181 - 3.186. *Cienfuegosia ulmifolia*, development of the gynoecium and midstage floral characteristics. Bars = 200 μm in 3.181 - 3.184, = 2 mm in 3.185, = 50 μm in 3.186. 3.181. Partially dissected androecium. The tissue below each of the oldest common stamen primordia has elongated. The gynoecium consists of three carpel primordia in a single spatial whorl. Each of these carpel primordia has an adaxial crevice. There is a very small apical residuum in the center of the gynoecial whorl. 3.182. Oblique polar view of young gynoecium. The three carpels have completely fused at the base and midsection of the column; the only evidence of the individual members is the three apical lobes. 3.183. The apical portion of the gynoecium has surpassed the androecium in height. Some differentiation of the stigmas and anthers has occurred. The individual members composing the stylar column are not apparent except for the three stigma lobes. 3.184. Further development of the three sessile capitate stigmas. 3.185. Partially dissected flower bud prior to opening. The sepals have elongated beyond the other organs. The petals have formed a protective dome over the remaining floral organs. 3.186. Pollen grain prior to anther dehiscence. The pollen is spheroidal, spiny, and polyporate.
Initiation and early development of the gynoecium -- Carpel initiation occurs when the common stamen primordia are proliferating centrifugally. The three carpel primordia initiate in a single spatial whorl (Fig. 3.181). Based on equal size of the early primordia, the sequence of initiations is presumed to be simultaneous (Fig. 3.181). A small apical residuum persist interior to the young carpel whorl. Each carpel develops an adaxial crevice (Fig. 3.181) and then a locule. As the gynoecium enlarges and elongates, the carpel bases fuse into a syncarpous ovary (Figs. 3.179, 3.182). As the apical portions of the carpels elongate, they fuse into a single stylar column with the individual members only evident by the three lobes at the apex (Figs. 3.179, 3.182). By the time the stylar column has surpassed the androecium in height, differentiation of the three stigmatic lobes has begun (Fig. 3.183).

Midstage reproductive characters -- There is no evidence of the bractlets on the flower buds. The calyx does not arch over and form a dome over the other developing organs. The bases of the sepals fuse, but the apical portions elongate upward and extend greatly beyond the remaining flower bud (Fig. 3.185). In the young and midstage flowers, the petals form tightly sealed domes over the remaining floral organs (Fig. 3.185). The petal bases are ontogenetically fused to the base of the androecium (Fig. 3.185).

In the young and midstage flowers, the anthers diverge in partially fused pairs from the androecial column (Fig. 3.180). Five small sterile teeth are present at the apex of the androecial tube. The stylar column is surmounted by a tripartite capitate stigma, i.e. three sessile capitate stigmas (Fig. 3.184). Several ovules develop in each locule. The pollen is spheroidal, spiny, and polyporate (Fig. 3.186).
DISCUSSION

The involucel -- Several characteristics of the involucels are variable among the taxa in these two tribes. All of the members examined in the Hibisceae have more than four (between four and 14) bractlets per flower, and the number is variable within a species. The taxa examined in the Gossypieae all consistently initiate three bractlets per flower, but in some species they don't persist through floral development. In the case of *Thespesia populnea*, the bractlets generally persist and continue to develop at least until all of the other floral organs have initiated and begun to differentiate, but they fall off before the flower buds reach mature size. The bractlets in *Cienfuegosia ulmifolia* are suppressed very early; the primordia fail to enlarge significantly or differentiate and they are not apparent by the time the petals initiate.

According to Fryxell (1979, 1988, 1997), most species of *Cienfuegosia* have an involucel, only four species (including *C. ulmifolia*) lack involucels. He reported the merosity of the bractlets (when present) is typically nine to 12, rarely reduced to three due to coalescence or lateral connation. Clearly, *C. ulmifolia* only initiates three bractlet primordia and there is no evidence of more numerous primordia fusing to produce three. Fryxell's idea is one that needs to be further investigated for the other species of *Cienfuegosia*, and SEM would be a good tool to elucidate the bractlet ontogeny. It would be interesting to see if some species of *Cienfuegosia* have common bractlet primordia that trifurcate as is *Radyera*. In addition, the other taxa that are described as lacking involucels should be examined to see if the bractlets are initiated and suppressed in some way as they are in *C. ulmifolia* and *T. populnea*. The suppressed bractlets in these two taxa may be evidence of a transitional stage in loss or gain of bractlets.
A bractlet ring meristem is not consistently present among taxa. The involucel appears to initiate on a low ring meristem on the floral apex in *Hibiscus lasiocarpos* and *Kosteletzkya virginica*, but in the other taxa where early initiation has been studied, there does not appear to be a bractlet ring meristem. Only one species examined in this paper, *Radyera farragei*, has connate bractlets at maturity. The presence of a bractlet ring meristem and connation were also variable characteristics in the Malvavisceae (Ch. 2). The presence of a ring meristem does not appear to correlate with bractlet fusion.

Payer (1857) described the members of the "calicule" as all arising as distinct bulges (no ring meristem) and that any connation occurs after initiation. He also discussed how the work of Duchartre (1845) alluded to the presence of a bractlet ring meristem that later becomes separated into primordia. Since the bractlet ring meristems, when present, are not always very pronounced and do not always persist, this character can only be determined by viewing the stages of the floral apex just prior to initiation of bractlet primordia.

All of the taxa examined have helical initiation of bractlets on the floral apex, but it is more complex in *Radyera farragei*. In this species, rather than bractlet primordia initiating individually, common primordia initiate helically, then subsequently become lobed and divide. Helical bractlet initiation was also found in cotton by Gore (1935) and in *Hibiscus acetosella* by Ault (1987).

Payer (1857) believed that the bracts and bractlets were both homologous to leaves and stipules. He did not distinguish between floral bracts (which subtend floral apices) and involucellar bracts or bractlets (which occur on floral apices). He believed that the "calicule" (involucel) was formed by "bractées" and their accompanying "stipules". He believed that "calicules"
with numbers other than three were formed by a single flower having more than one "bract" and "stipule" pair, and by two stipules fusing to become one member. He described the order of initiation for the "bractées" in *Kitaibelia vitifolia*, *Pavonia hastata*, and *Hibiscus syriacus* with two opposite members arising first, then "lateral stipular members" arising later. In the taxa I examined in the Malvavisceae (Ch. 2) and in examining the few illustrations of bractlet initiation provided by Payer (1857), the bractlets appear to initiate in a helical sequence. There is no indication of the bractlets arising in groups of three (one large followed by two lateral smaller ones). Even in *Radyera*, the bractlets arise first as common primordia, then become unequally three-lobed, with the lobing pattern more similar to a single three-lobed bract than a bract and accompanying floral stipules. For the reasons I outlined in chapter 2, the bractlets are more likely homologous to sepals than to leaves; but, rather than being considered as an extra set of sepals, they should be considered as a whorl of discrete floral organs.

An unusual feature of the involucel in *Thespisia populnea* is that the bractlets are not all at the same level on the receptacle. Similarly, the bractlets are described as inserted in a more or less irregular spiral arrangement in a few species of the Gossypieae, not only *T. populnea*, but also *Thespisia beatensis*, *Lebronnecia kokioides*, and *Hampea rovirosae* (Fryxell, 1979). In the Malveae, *Mavella leprosa* (Fryxell, 1988) and several species of *Callirhoe* (Dorr, 1990) and *Anisodontea* (Bates, 1969) are described with one or more members of the involucel separated from the base of the calyx. The ontogeny of *Callirhoe involucrata* var. *involucrata* and *Anisodontea X hypomandarum* will be examined in chapter 4.
Preliminary results indicate that in these taxa, the bractlets initiate on the floral apex in a pattern similar to *T. populnea*.

In the taxa with mature bractlets, the involucel is green and shorter than the corolla. The shape of the mature bractlets is variable among taxa, ranging from linear in *Hibiscus lasiocarpos* and *Kosteletzky virgina* to very broad in *Gossypium hirsutum* and fused in *Radyera farragei*.

**Calyx** -- Several features of the calices are variable among taxa. All of the taxa examined have at least some basal fusion of the sepals, but the amount varies from 1/4 to 1/3 in *Kosteletzky virgina* to complete fusion in the calyx cup in *Thespesia populnea*. The basal fusion of the sepals appears to occur a little later in floral development in *Radyera farragei* than in the other taxa.

In most taxa, the sepals arch over and form a temporary protective dome over the remaining floral organs in a young bud. *Cienfuegosia ulmifolia*, in which the involucel is suppressed, is the exception to this generalization. The petals in *C. ulmifolia* form the protective dome and the sepals remain apically separated and extend beyond the young corolla dome in a way that is typical of bractlets in most malvaceous floral buds. Later, the sepals converge inward but the lobes remain distinct and form a projection above the major portion of the bud. It seems, therefore, that the sepals take up the role of the suppressed bractlets and the petals the usual role to the sepals temporarily in early floral development, then assume their usual roles in late floral development.

The initiation of a sepal ring meristem is not a consistent feature in either tribe. A low ring meristem develops before the sepal primordia, or at least before most of the primordia initiate in all the taxa except *Radyera*.
farragei and Cienfuegosia ulmifolia. Both Gore (1935) and Moncur (1981) described the calyx in cotton (Gossypium) as first initiating as an undulating collar which grows more rapidly at five definite points. Payer (1857) stated in regard to the calyx that the free parts appear first, and the fused parts later. He declared that exceptions to this are found in Malvaceae members which lack "calicules" (involucels); in these cases the sepals arise by a common membrane. My results do not support this synopsis by Payer. Of the taxa that have involucels, most have sepal ring meristems; and Cienfuegosia ulmifolia, with an initiated but suppressed involucel, does not have a sepal ring meristem.

The three Gossypieae examined in this research have helical initiation of the sepals. Most of the Hibisceae have a simultaneous order of initiation in the sepals; Radyera farragei is the exception in having a helical sequence of initiation. Ault (1987) described the sepals as initiating more or less concurrently in another member of the Hibisceae, Hibiscus acetosella.

**Petals** -- Other than variations in color and perhaps petal shape and size, the mature characteristics of the corollas were very similar for the taxa examined in both tribes. All the species examined have a five-merous contorted corolla which extends beyond the calyx and beyond the involucel (if present), and that flares to form an open showy flower. The petals in each taxon are distinct, lack auricles, and are basally connate to the base of the androecium.

All of the taxa initiate a petal-stamen ring meristem prior to petal initiation. Most of the taxa also initiate five common petal-stamen mounds or regions, although they are not always well defined and do not always persist as the petal-stamen ring meristem enlarges. This feature was particularly
difficult to determine with any certainty in *Abelmoschus manihot* and *Gossypium hirsutum*, and was not determined for *Thespesia populnea*. In all the taxa examined, the order of initiation of the petals is simultaneous and petal position is alternate to the sepals. When it could be determined, the petals appeared to initiate at the same time as the first partitioning event of the androecial portion of the ring meristem. Petal elongation is generally delayed until all of the common stamen primordia have initiated.

**Relationship between petals and stamens** -- The formation of a petal-stamen ring meristem in Malvaceae has been disputed in the literature. Payer (1857) and van Heel (1966) described malvaceous flowers with ring meristems on which petals and stamens form. Others have documented the formation of a ring meristem in cotton (Gore, 1935; Moncur, 1981) and in *Hibiscus cannabinus* (Moncur, 1981). In *Hibiscus acetosella*, Ault (1987) described a ring meristem shared by petals and stamens but with the petals initiating prior to formation of the ring meristem. Sattler (1973), in examining two members of the Malveae, did not find a petal-stamen ring meristem. He found that in both taxa the corolla initiated as five distinct primordia and that adnation of the petals to the androecium occurs later by growth in the zone below the petals. In *Malva neglecta*, he described the androecium initiated first as a ridge, then primordia appeared. In *Alcea rosea*, he detailed the initiation of five stamen primordia followed by interprimordial growth forming a "girdling androecial primordium". I not only found the formation of a petal-stamen ring meristem in Hibisceae and Gossypieae, but also in the Malvavisceae (Ch. 2). In chapter 4, I intend to look at the ontogeny of members from the Malveae. Hopefully, with the high resolution provided by.
SEM, I will be able to resolve whether a common petal-stamen ring meristem forms in the Malveae as well.

Common petal-stamen primordia are not as uncommon as one might think; they have been found in many other plant families (Ch. 2). I found common petal-stamen primordia in the Malvavisceae (Ch. 2) and in most members of the Hibisceae and Gossypieae, although in some taxa it was quite difficult to ascertain. Payer (1857) and Sattler (1973) did not see formation of any common petal-stamen primordia in members of the Malvaceae. Van Heel (1966) may have alluded to the presence of common petal-stamen primordia in some taxa. He described the corners (alternate to the sepals) of the "peripheral wall" (petal-stamen ring meristem) as elevated prior the initiation of petals and stamens. Ault (1987) did not describe the formation of common petal-stamen primordia in *Hibiscus acetosella*; however, I question his interpretation of when petal initiation has occurred. In looking at Ault's micrographs, what he described as petal primordia (his Fig. 16), I interpret as common petal-stamen primordia, these subsequently dividing into petal and common stamen primordia (his Fig. 17). Gore (1935) did not see common petal-stamen primordia in cotton. Differences in the interpretations of researchers concerning the formation of common petal-stamen primordia may be due to taxon differences or to differences in the techniques used; light microscopy does not give the same resolution as SEM. Also, according to Ronse Decraene, Clinckemaille, and Smets (1993), observation of common petal-stamen complexes can be very difficult, and critical stages are often missed because the primordia divide rapidly and the petals sometimes develop very slowly. This difficulty in observation is compounded in some Malvaceae by the fact that after the five common petal-stamen mounds
initiate, they may become less defined with enlargement of the ring meristem as in *Hibiscus lasiocarpos* and *Radyera farragei*. In some cases, the mounds were either apparent for such a short time that the critical stage could easily be missed or they were too poorly defined to be diagnosed with any certainty, as in *Abelmoschus manihot* and *Gossypium hirsutum*.

The literature is contradictory as to whether the petals or the stamens initiate first in Malvaceae. Payer (1857) described the petals in malvaceous flowers as appearing before the stamens. He commented that Duchartre (1845) was probably in error in saying that the stamens preceded the petals. Van Heel (1966) concluded that in Ureneae (Malvaviscæae) and Hibisceæ (which in his view included members of the Gossypieæ) the petals seem to arise before any stamen primordia, but in Malveæ the petals arise when some of the stamen primordia are present. Sattler (1973) reported the petal primordia and the first five members of the androecium as appearing at the same time (or nearly so) in two taxa in the Malveæ. Gore (1935) described the petals in cotton as occurring at the same time or after the first evidence of stamen divergence. Petal initiation has been described as preceding stamen initiation in *Hibiscus cannabinus* (Moncur, 1981) and *Hibiscus acetosella* (Ault, 1987). Part of the conflict over the sequence of inception may be due to confusion in identifying common petal-stamen mounds; some researchers, Ault (1987) for example, may have erroneously interpreted these structures as petals. Also, initiation of these two organ whorls occurs very rapidly and critical stages may be easily overlooked. In addition, comparing the size of the petal primordia and the early common stamen primordia is not a reliable way to determine the sequence of inception since petal enlargement is retarded during stamen proliferation. I found that the petal primordia initiate
concurrently or nearly so with the first common stamen primordia (or first staminal partitioning event) in the Malvavisceae (Ch. 2), Hibisceae, and Gossypieae.

**Androecia** – Merosity of the stamens varies among taxa and even within a species. In general, members of these two tribes, Hibisceae and Gossypieae, have androecial columns with numerous stamens (averaging over a hundred). *Kosteletzkya virginica* is the exception with approximately 40 androecial members. *Thespesia populnea* has the most stamens with an average of 200. Large numbers of stamens were also found in cotton (50 to 125 stamens) by Gore (1935) and in *Hibiscus acutifolius* (59 - 73 stamens) by Ault (1987). In contrast, representatives in the Malvavisceae usually have between ten and 50 stamens (Ch. 2). Examinations of many more taxa are needed to determine if low stamen numbers are typical of all Malvavisceae and higher numbers are typical of most Hibisceae and Gossypieae.

Little variation was found for many of the mature androecial characteristics for members of Hibisceae and Gossypieae. All of the taxa have androecial columns that are shorter than the corollas. Stamen filament divergence is radial and generally occurs throughout the length of the column. Mature androecia have elongated filaments and none of the filaments are retrorse. In *Hibiscus lasiocarpos* and *Kosteletzkya virginica* the tip of the androecial column may be bent upward along with the gynoecial styles in flowers positioned somewhat horizontally. Some of these mature characters were found to be quite variable among members of the Malvavisceae (Ch. 2).

The pattern of filament divergence was a variable character among taxa. In *Hibiscus lasiocarpos*, *Radyera farragei*, and *Gossypium hirsutum* the
filaments may diverge singly or in pairs; and in *Kosteletzkya virginica* and *Abelmoschus manihot* single divergence is typical. *Thespesia populnea* and *Cienfuegosia ulmifolia* typically have filaments that diverge in pairs, and some or all of the paired filaments may be partially fused. Partially fused stamen pairs were also found by Ault (1987) and van Heel (1966).

Generally, five apical androecial teeth are initiated in each flower; but in *Thespesia populnea*, the teeth can become lobed or deeply dissected so that it may appear that there are more than five teeth that are irregular in height and spacing. In *Radyera farragei* the androecial column appears to have a variable number of unequally-sized and spaced sterile teeth. The teeth can be very small and triangular as in *Gossypium hirsutum* or long and filamentous as in *Thespesia populnea*.

**Stamen proliferation and bifurcation** -- The pattern of early stamen proliferation varies among taxa. Prior to petal initiation, there appear to be five common petal-stamen mounds. At the time the five petal primordia initiate, however, these common petal-stamen mounds may be well defined or more commonly become less evident with the enlargement of the petal-stamen ring meristem. In most members of the Hibisceae and Gossypieae, the five common stamen mounds or regions divide laterally to yield a total of ten common stamen primordia in most representatives, or fifteen in *Thespesia populnea*. *Kosteletzky virginica* has five very irregularly-shaped common stamen primordia in the early stage; these could be interpreted as ten primordia with the separation not very clear between the lateral pair in each sectorial region. These five irregularly-shaped common stamen primordia in *K. virginica* subsequently divide to yield a total of 15 common stamen primordia, three staggered in each sectorial region. After the previously
described stages, proliferation in both tribes continues in a centrifugal direction until numerous common stamen primordia have initiated.

The earliest stage of androecial development with the five common androecial mounds has sometimes been missed by early researchers. Payer (1857) stated that after formation of the ring meristem, one sees at first ten furrows which divided the androecium into ten equal parts. In some of his figure legends, however, he described five common staminal humps or five connate androecial primordia prior to formation of ten androecial mounds. Similarly, van Heel (1966) detailed the initiation of ten androecial mounds on the ring meristem, but he stated that "sometimes the number of staminal buttresses seems to be limited to an initial five," which subsequently divide "superficially into two collateral parts". Gore (1935), Sattler (1973), and Ault (1987) reported that the sequence of early initiation of the androecium proceeds from five androecial mounds to ten mounds; and that this increase results by the lateral division of the original five mounds into ten mounds or by the initiation of five other mounds alternately in the same whorl as the first mounds. All of the above-mentioned researchers concur that after the initiation of these ten common stamen mounds at the apex of the androecium, initiation of subsequent common stamen primordia occurs in a centrifugal direction.

All of the members examined in the Hibisceae typically have ten radial rows of centrifugally initiated common stamen primordia, two rows in each sectorial region on the ring meristem. The androecium has five leading and five alternating lagging rows of common stamen primordia. Typically, at the stage when there are ten common stamen primordia on the ring meristem, the leading rows originate from the common primordia that are larger or radially
broader than the common primordia that begin lagging rows. When centrifugal proliferation of the common stamen primordia begins, the leading rows usually initiate common stamen primordia earlier and start more interior on the ring meristem than the lagging rows. In addition, leading rows may initiate the same number or more common stamen primordia than the lagging rows. 

*Radyera farragei*, while it has the size difference and the earlier proliferation, is the exception in that the leading rows do not appear to be significantly more interior on the ring meristem. In the Gossypieae, *Cienfuegosia ulmifolia* has the common stamen primordia typically arranged in ten centrifugally initiated radial rows, with five leading and five lagging rows. *Gossypium hirsutum* deviates from the five paired rows by frequently initiating one or three common primordia rather than a lateral pair. Despite these sometimes numerous aberrations, the overall pattern is ten radial rows. Also, in *G. hirsutum*, the distinction between the leading and lagging rows is not very pronounced. *Thespesia populnea* does not have ten radial rows of common stamen primordia. Rather than the common primordia in each sectorial region of the androecium initiating centrifugally in lateral pairs, they initiate centrifugally in lateral or oblique triplets or quads along part of the length of the column, switching to lateral pairs only at the base of the column with the last formed organs. With the lateral or oblique bifurcation of most of the common primordia and elongation of the column, the mature androecium in most taxa appears to have 20 longitudinal rows of stamens. *T. populnea* would appear to have more than 20 stamen rows (although not typically in discrete linear rows) in portions of the androecium.

In my examination of the Malvavisceae (Ch. 2), I found that stamen proliferation is much more complex and variable than in the Hibisceae.
or Gossypieae. In most Malvaviscæae, stamen numbers (in particular common stamen numbers) are so small that the term radial rows cannot be applied. Generally, in taxa with larger numbers of stamens, the common stamen primordia can be aligned in ten reduced radial rows but the order of initiation is not strictly centrifugal. The initiations of common stamen primordia in members of this tribe may occur in centrifugal, centripetal, or oblique directions. Also, in some taxa rather than the common stamen primordia in each sectorial region initiating in lateral or nearly lateral pairs, the common stamen primordia in the paired rows initiate in more of a stair-step pattern. In addition, bifurcation of these common stamen primordia can occur in a radial, lateral, or oblique direction. The directions of the bifurcations play a big role in determining the final placement of stamens on the column. In general, it seems best to categorize the proliferation of stamens in this tribe as highly modified and much more variable than in Hibisceæae and Gossypieæae.

The early literature with regard to the number of stamen rows is often confusing. Part of the confusion is due to inconsistency in qualifying which primordia are common primordia that will subsequently divide, and which ones are distinct primordia that do not divide further. For example, Payer (1857) described the androecial column with ten series of stamen primordia which arise from the top to the bottom; after all of the stamen primordia have been formed, each divides into two others. Even in describing mature stamens there is confusion. For example, van Heel (1966) describes "the rows of stamens as a rule formed by single forked stamens" and in some taxa "only half-stamens seem to leave the tube." In general, ten rows of stamen primordia have been described for some members of the Malvaceæae by Payer (1857), Gore (1935), van Heel (1966), Sattler (1973), and Ault (1987).
More numerous radial rows of common stamen primordia on part or all of the column are pictured or described in some way in *Alcea rosea* (van Heel, 1966; Sattler, 1973) and in *Abutilon darwinii* (van Heel, 1966).

Van Heel (1966) and Ault (1987) used the terms "major" and "minor" rows rather than leading and lagging. Van Heel (1966) also discussed how the stamen rows are not truly radial in the androecium because the rows may approach the petal radii near the base of the column, and approach the sepal radii near the top of the column. He stated that in the middle or upper parts of the androecial tube the rows are placed equidistantly or almost on the sepal radii and in the lower parts they may be placed more in front of the petals. Although I noticed this character, I chose not to elaborate on it with reference to each taxon. I use the term "radial" loosely, to mean that the rows diverge from the center in a course that is generally near the radius. I do not use it to imply that the rows are perfectly straight or equidistant from each other the entire length of the column.

I make the distinction between initiations of primordia or common primordia from a common meristematic sectorial region (i.e. partitioning) and the bifurcations (i.e. splitting) of common primordia. In a malvaceous androecium, many common stamen primordia may arise from each of the original five common stamen mounds or regions in a variety of sequences. These common stamen primordia may appear to result from radial or lateral divisions of the original mounded areas or they may appear as individual primordia on unoccupied spaces in each region. With bifurcation, a common primordium becomes elliptic in shape, then apically peanut-shaped with a slightly elevated base, and finally gives rise to two stamen primordia.
In the Hibisceae and Gossypieae, these bifurcations appear to result in equal-sized lobes and thus equal division of the common primordia. In most taxa in which bifurcation of common staminal primordia has been reported, the resulting two lobes are equal in size (Bayer and Hoppe, 1990; Ronse Decraene and Smets, 1993). In the Malvavisceae, the bifurcations may be equal or unequal (Ch. 2). Unequal bifurcations of common stamen primordia have also been described or illustrated in some members of the Malvavisceae by Payer (1857) and van Heel (1966), and in Actinidiaceae by van Heel (1987).

Previous researchers have attempted to attribute the formation of bisporangiate or "half-anthers" to the bifurcation of common stamen primordia. Payer (1857) attributed the unilocular anthers in *Lavatera olbia* as to division of each bilocular stamen into two. Yet in *Pavonia hastata*, he described the stamen primordia dividing more than once without any change in anther locule number, though he did not distinguish between partitioning and bifurcation. Saunders (1936) looked at the vascular system in the androecium. In *Corydalis* (Fumarioideae), she stated that "if the vascular complement proper to a floral member is halved before the bundle is fully organized and delimited from the vascular elements appropriated to other whorls, and if the two halves do not reunite, then the corresponding floral member will be replaced by two separate half-members." In the Fumarioideae, after the first halving, there is no subsequent division of the bundles, therefore only one pair of half-stamens replaces what would be a whole stamen. Saunders further claimed that subsequent splitting of half strands after they have become isolated (i.e. after the determinate phase has been reached), will not result in further fractionization of the organs, but in the multiplication of the product of the
original bipartition. She claimed that in Malvaceae, repeated division usually occurs after the first halving, thus explaining why a large number of half-stamens are produced in place of a single whole stamen. Rao (1952) was not convinced by Saunders' explanation. He found that the staminal traces in members of the Malvales divide into three bundles regardless of whether they make dithecous or monotheceous stamens; the only difference is the level at which branching occurs. He was not persuaded by her argument that only the primary and not the secondary division results in fractionalization. Van Heel (1966) believed that half-stamens were actually the result of serially split stamens, the branches of which are inserted on the androecial tube. He justified this by the occurrence of other half stamens that occur distinctly in pairs (paired divergence of filaments). He did not attempt, however, to correlate directly the single or paired condition of the stamens on a mature flower with early ontogeny. Both Saunders' and van Heel's hypotheses do not take into account how the bisporangiate condition arises in stamens that do not result from a bifurcation, i.e. primordia that arise independently in their sector of the ring meristem and never undergo a division; a situation I found in some Malvavisceae (Ch. 2). In members of the Malvavisceae, some stamen primordia do not bifurcate, and some bifurcate once, yet all of the anthers are typically bisporangiate. Ronse Decraene and Smets (1993) describe a similar type of "dedoublement" (doubling) in Theobroma cacao (Sterculiaceae), in which only one of the two original stamen whorls bifurcates.

In the Hibisceae and Gossypieae, I found that most of the common stamen primordia bifurcate and do so only once. In some taxa, the last androecial members to form on the column may not bifurcate. It appears that these latent members may form sterile filaments or bisporangiate anthers; I
have not seen any tetrasporangiate anthers in these taxa. Gore (1935) claimed that in cotton the members of the ten rows of stamen primordia (except the bottom members) divide one or more times. In *Hibiscus acetosella*, Ault (1987) found that most of the common stamen primordia bifurcate. He reported that the last-formed androecial members at the base of the column may divide and develop into a stamen pair, develop into a single stamen, or form a filament without sporangia. He did not specify whether the single stamens are bisporangiate or tetrasporangiate.

The number of times that the common primordia bifurcate is an important issue. If bifurcation causes the reduction in sporangia from four to two per anther, then one might assume that each common primordium should divide once and only once; otherwise we might obtain anthers that are unisporangiate or tetrasporangiate. However, the common stamen primordia may bifurcate once, not at all, or several times without change in the sporangia number (the latter indicated by Payer (1857) and van Heel (1966). Ronse Decraene and Smets (1993) even reported in *Ricinus* (Euphorbiaceae) that the process of splitting "can be repeated ad infinitum." Therefore, bifurcation does not correlate with the bisporangiate condition. So what about the idea suggested by Saunders (1936), that it is an early division that establishes the bisporangiate condition? Rather than looking at the first bifurcation, let's consider earlier divisions of the common stamen mounds on the androecial ring meristem. In some taxa the first five common mounds are each divided laterally by furrows into two primordia; but in some taxa, like *Thespesia populnea*, the first five common mounds are each divided laterally into three primordia. In *Malachra capitata*, the first five common stamen mounds bifurcate. So early partitioning of the androecial regions can occur by one
division or two simultaneous divisions, or bifurcation can occur, yet all result in an androecium with bisporangiate anthers. In addition, each sectorial region of the androecial ring meristem can initiate many common stamen primordia in a variety of different patterns. Therefore, Saunders' hypothesis that early divisions correlate to the "half-anthers" does not hold true. In summary, neither early divisions of the androecium nor bifurcations are likely responsible for the bisporangiate condition; but rather, these processes are simply a means of proliferation of the bisporangiate condition.

In some taxa, the filaments of two stamens are partially fused. This was common in *Thespesia populnea* and *Cienfuegosia ulmifolia*. In these taxa, basal connation of the filaments above the point of attachment to the androecial tube may be attributed to several factors. First, there can be exaggerated elongation of the base or stalk supporting a peanut-shaped common primordium prior to bifurcation. Secondly, the bifurcation may affect just the apical portion of the common primordium, leaving a common zone below. Lastly, after bifurcation, elongation of the filaments can occur mostly above or below the point of common divergence. If elongation occurs above this point, the filaments may appear distinct but very close together on the androecial column. The closeness of these paired filaments is dependent on how the androecial column elongates. Elongation of the androecial tube below where the filaments diverge results in the filaments remaining close together, whereas elongation of the tube at the level of filament divergence results in a less obvious association between the paired filaments. If elongation of the filaments occurs below the point of common attachment or by one of the other methods described, then the filaments appear fused to some extent. Partially fused filaments between stamen pairs have also been
reported in Malvaceae by Ault (1987) and van Heel (1966, 1969) and in other plant families by Davis and Mariamma (1965) and Ronse Decraene and Smets (1993).

Most species examined have the common petal-stamen mounds and thus the common stamen groups basically opposite the petals. *Thespesia populnea* (Gossypieae) and *Malachra capitata* (Malvaviscæ, Ch. 2) have common stamen mounds or stamen sectorial regions that are alternate to the petals. The position of the stamen groups in regard to the petals is not always clear cut. There are several gradations between these two states. Some of these taxa may have stamen groups that are slightly off-center to the petals. Several factors make characterizing position of these two organ groups difficult. First, the early petal primordia are lop-sided according to the direction of petal contortion. Also, the petal primordia initially do not broaden or elongate much in relation to the androecium; therefore, the stamen groups may be wider than the adjacent petals. The petals may be positioned on the same radii as the stamen groups or slightly to one side; or as in the case of *Thespesia* and *Malachra*, they may be alternate. Also, as the petals begin to enlarge, they may broaden radially more to one side than the other, depending on the direction of petal contortion. A good example of this situation was reported by Gore (1935) when he described cotton with staminal lobes alternate with the petals at an early stage, "but with later growth and twisting of the petals the staminal lobes appear opposite the petals." Another factor that complicates determining position of the stamen regions is that as the androecial column elongates, the stamen rows may be on different radii at the base and the summit of the column, as noted by van Heel (1966). Van Heel (1966) found that in most taxa, the stamens are opposite to the
petals (alternisepalous). Similar to my findings, his description of *T. populnea* places the five staminal elevations in alternipetalous positions. Payer (1857) reported the stamens as opposite (superposed) to the petals. Sattler (1973) described the early stages of the androecium with five pairs of stamen primordia opposite the petals in *Alcea rosea*; but in *Malva neglecta*, he reported five stamen primordia opposite the petals and five opposite the sepals. It appears that, depending on which stage of development the researcher is looking at, different conclusions may be made in regard to stamen group positions.

All of the taxa examined in the Hibisceae and Gossypieae, as well as Malvavisceae (Ch. 2), have sterile teeth at the apex of the androecial tube, but the origin and position of the teeth are variable. In most taxa, there is space left in front of the stamen primordia on the surface of the androecial ring meristem. This meristematic tissue elongates and forms at least a portion of the sterile teeth. In taxa where there is no obvious unused space in front of the stamens, sterile teeth can still form from tissue on the interior surface of the ring meristem. In most cases, the sterile teeth are in line with the stamen groups, i.e. one tooth originates from the interior surface of each common stamen region. Three members of the Malvavisceae apparently do not have the teeth in line with the stamen groups (Ch. 2). This character is very hard to determine for several reasons. First of all, by the time the teeth initiate, the androecial column has started to elongate, the distinction between stamen groups is less clear with crowding of the stamen primordia, and the petals have broadened and may even overlap. In addition, the sterile teeth usually do not initiate exactly on the radii of the stamen groups; they often initiate off-center where there is space remaining in front of the lagging stamen rows.
The literature is contradictory about the position of the sterile teeth as alternate or opposite the petals. Saunders (1936) emphasized that in no case is there an antesepalous whorl present in the androecium. In her opinion, all of the fertile stamens correspond to a single whorl of five antepetalous members, the primordia of which have undergone primary collateral splitting and have thus given rise to many half-stamens. The taxa examined by Saunders (1936) supposedly have teeth opposite to the petals. Therefore, she asserted that the teeth are terminations of the five fertile antepetalous members, and not the aborted sterile antesepalous whorl of the androecium as suggested by previous investigators. Even though most of the teeth are non-vascular, Saunders found two varieties of *Hibiscus rosa-sinensis* that have vascular bundles in the teeth that result from prolongation of the vascular bundles of the antepetalous group of stamens. Similar to my results, van Heel (1966) reported that in some taxa, the sterile teeth are positioned alternate to the petal radii and in other taxa they are opposite the petal radii. The finding of some taxa that have stamen groups and sterile teeth that are alternate with the petals, such as *Thespesia populnea*, may refute Saunders' hypothesis. More ontogenetic work is needed before the homology of the sterile teeth can be ascertained in the Malvaceae.

Several factors are responsible for the large number of stamens in the Hibisceae and Gossypieae. First of all, there is the formation of an androecial ring meristem. Endress (1994) stated that in flowers with a ring-like androecial mound, the gynoecium appears before the individual stamens or at least before the last stamens (the latter is the case in Malvavisceae). According to him, this delay in initiation of individual stamens allows the floral apex to expand, so that the androecial part of the floral apex is separated from the
gynoecial part by a furrow and proliferates in the form of a ring-mound. Many other angiosperms give rise to many stamens from ring meristems (Ronse Decraene and Smets, 1991, 1992; Endress, 1994).

Another factor that contributes to the large numbers of stamens in Malvaceae is the partitioning of the ring meristem into many common stamen primordia, i.e. the radial or lateral proliferation of common stamen primordia in each mounded area or sectorial region on the ring meristem. Ronse Decraene and Smets (1987, 1992) described this process of proliferation as complex or secondary polyandry. They distinguished complex polyandry as secondarily acquired stamen multiplication in an oligandrous framework. Endress (1994) described secondary polyandry, where a low number of primary primordia often secondarily subdivide to give rise to a higher number of secondary stamen primordia. The term secondary primordia has various connotations in the literature. Endress (1994), in describing Kitaibelia, referred to the initial common stamen primordia on the ring as primary primordia and referred to all stamen primordia that initiate thereafter (regardless of their numbers, position, or order of initiation) as secondary primordia. Sattler (1973) and Ault (1987), used the term primary for the first set of stamen primordia, secondary for all ten primordia that result from the lateral division of the primary, tertiary for all primordia that initiate centrifugally from the secondary (regardless of the number of outward sets and their order), and quaternary to represent all primordia that result from the lateral division of tertiary primordia. Regardless of the terminology, a secondary increase of stamens has been reported in many plant families (Ronse Decraene and Smets, 1987, 1992; Bayer and Hoppe, 1990; Endress, 1994).
Bifurcation of common stamen primordia also contributes to the large stamen numbers. The processes of bifurcation and partitioning of common stamen primordia have often been confused in the literature and have been collectively called serial splitting, doubling, or dédoublement. Ronse Decraene and Smets (1993) discussed the controversy about using the term "dédoublement," which originally was used to describe the process of doubling of a stamen primordium to two equivalent primordia, but subsequently was used to explain the occurrence of higher stamen number, even without evidence of a division. They interpreted dédoublement or chorisis in a strict sense, to describe the division of a primary primordium into two or more units with the implication that all of the primary primordial tissue is used up in the formation of the two or more daughter primordia. They described that "such development is different from the progressive filling-up of virgin space on protuberances or on complex primordia by secondary primordia, or the covering of a hypanthium with numerous stamens." They proposed to "restrict the use of the term dédoublement to only those cases where two stamens are found replacing a single stamen by increase, either as two independent entities or by the lateral splitting of a primordium." They offered the term "polygenesis" to apply to a situation when a larger number of stamens is produced by complex primordia, a ringwall, or a hypanthium. In my analysis, Malvaceae exhibits both polygenesis and dédoublement, though bifurcation is a more specific term for the kind of dédoublement.

High numbers of stamens are found in many other plant families besides Malvaceae, and there are several ontogenetic pathways to multistaminy (Payer, 1857; Gemmeke, 1982; Ronse Decraene and Smets, 1987, 1992, 1993; Weberling, 1989; Derstine and Tucker, 1991;
Endress, 1994). Stebbins (1974) suggested that "the adaptive value of an increased number in stamens is to provide an excess of pollen beyond that required for fertilization." He based this conclusion on the fact that most flowers that have very large numbers of stamens are relatively flat, have little or no nectar, and are attractive to pollen-gathering vectors.

**Gynoecium** -- Some characteristics of the mature gynoecium vary among taxa. In most Hibisceae the gynoecium is five-merous, but the collection of *Abelmoschus manihot* used in this study is unusual in having ten carpels. Five of the carpels are slightly taller than the five alternate carpels. Members of the Gossypieae generally have three to five carpels; *Cienfuegosia ulmifolia* typically has three carpels. Only *Hibiscus lasiocarpos* and *Kosteletzkya virginica* have styles that diverge apically from the gynoecial column. Also, in these two taxa the terminal portion of the mature gynoecium bends upward. The rest of the taxa have their styles fused the entire length, and in *Cienfuegosia ulmifolia* the individual styles are not discernible along the length of the column. The stigma type is capitate in the Hibisceae, compared to capitate and decurrent in the Gossypieae.

Several features of the gynoecium are consistent among all taxa examined. A small apical residuum remains in the center of the young gynoecial whorl. If not already connected by a basal ring meristem, the carpel bases quickly fuse and form a syncarpous ovary. The tips of the young carpels grow inward towards the center of the flower and fuse into a stylar column. The ovary is superior with axile placentation.

Early initiation of the gynoecium involves a carpel ring meristem in some taxa. Both *Gossypium hirsutum* and *Thespesia populnea* in the Gossypieae have low carpel ring meristems. The members of the Hibisceae
do not appear to have a carpel ring meristem prior to carpel initiation. It should be noted that this critical stage of carpel initiation was not observed in *Cienfuegosia ulmifolia* or *Abelmoschus manihot*. In the Malvavisceae, no evidence of a carpel ring meristem was found (Ch. 2).

Payer (1857) did not report a carpel ring meristem in the malvaceous taxa he examined; however, he did not examine any members of the Gossypieae. Gore (1935), similar to my findings, described the carpel primordia in cotton (*Gossypium*) as "first evident as a zonal meristem slightly raised at three to five definite points." Ault (1987) found that the gynoecial primordia in *Hibiscus acetosella* arise as five mounds on the periphery of a slightly concave apex. Van Heel did not find a carpel ring meristem in the Ureneae (Malvavisceae) (1978), but he described the complex gynoecium of *Kitaibelgia vitifolia* and *Malope trifida* (Malveae) as arising "as a continuous girdling meristem" (1995). Sattler (1973) examined two members of the Malveae and found that the gynoecium initiates as a rim in *Alcea rosea*, but in *Malva neglecta* it initiates as five primary primordia that subsequently form an almost even ridge by interprimordial growth.

Although the formation of a carpel ring meristem seems to vary among Malvaceous taxa, not enough taxa have been examined to determine if this feature could be used to help delineate the tribes. The formation of carpel ring meristems has often been missed in the early literature, especially in the Malvaceae where they are often very poorly defined and are quickly overtaken by primordia. So far, only members of the Gossypieae and some of the Malveae have been described with carpel ring meristems. This may change with further investigation using advanced microscopic techniques. Carpel ring meristems have also been reported in Papaveraceae and Capparaceae.
(Karrer, 1991; Endress, 1994), Gyrostemonaceae (Hufford, 1996) and Rosaceae (Evans and Dickinson, 1996).

In most representatives of the Hibisceae and Gossypieae, the carpels initiate in a single spatial whorl and the order of initiation is simultaneous. *Abelmoschus manihot* may be the exception. As previously mentioned, this plant collection has ten fertile carpels per flower, with five of the carpel primordia slightly smaller than the other five. All ten carpels appear to be aligned in a single spatial whorl. Similarly, two sizes of carpel primordia occur in a single spatial whorl in some representatives of the Malvavisceae (Ch. 2). The ten-merous gynoecium of flowers in the Malvavisceae arises as two sets (or whorls) of five primordia, but only one set forms fertile locules. Depending on the species, the sterile set of carpel primordia may develop invaginations or locules to some extent. Further investigation is needed for this collection of *A. manihot* to determine if the ten gynoecial primordia all initiate at the same time, or if they initiate as two sets similar to Malvavisceae. Flowers like this collection of aberrant *A. manihot* may help add insight about the transitions in the family from all fertile to some sterile carpels and in changes in carpel merosity, which can vary from three to numerous.

**Pollen and fruit** -- One character that has been used in the past to delineate the tribes has been fruit type. The Hibisceae and Gossypieae have capsular fruits where as the other tribes have schizocarps (Fryxell, 1968, 1975, 1988). Smith (1977) describes both schizocarps and capsules as derived from syncarpous gynoecia. He defines capsules as dehiscent and typically several- to many-seeded, and that rarely are they one-seeded. In schizocarpous fruits, the carpels separate from one another into 1-seeded indehiscent segments. It should be noted that many malvaceous
schizocarpous fruits have mericarps with more than one seed each (Fryxell, 1988, 1997). Most taxa I examined in the Hibisceae and Gossypieae contain several to numerous ovules per locule; Kosteletzkya virginica is the exception with only one ovule per locule. The capsules of Thespesia populnea are indehiscent according to Fryxell (1988). It is possible that the fruits in K. virginica and T. populnea may be evidence of transitional states between the two fruit types.

No attempt was made in this study to do a detailed analysis of the pollen grains. Therefore, pollen size, thickness, and aperture number, size, and position were not determined. Only general characteristics regarding the pollen grain shape, surface texture, and type of aperture were made. The shape of the pollen grains in most members of the Hibisceae and Gossypieae is spheroidal (or spherical). Radyera farragei had oblate to suboblate pollen. All of the pollen had spiny surface projections. Most of the taxa had porate apertures; the exceptions were Radyera farragei, Gossypium hirsutum, and Thespesia populnea with colporate apertures.

Comparative ontogeny and placement of certain taxa or tribes --
Most of the currently used morphological floral diagnostic features that distinguish the tribes are supported by findings of the current work. Members of both tribes have capsular fruits and a one to one ratio of stigmas to mericarps, and basically five teeth at the apex of the staminal column. The Hibisceae has five members in the gynoecium (except for one aberrant collection) and the styles may diverge apically from a partially fused stylar column or be fused their entire length. The Gossypieae has three to five gynoecial members and the styles are connate their entire length. Gossypol glands are apparent with the light microscope on various floral parts in the
members of the Gossypieae. Some of the diagnostic features (embryo characteristics and detailed pollen characters) were not scrutinized as part of this research.

Most of the ontogenetic characteristics such as order of organ initiation, presence or absence of ring meristems and common primordia, relative positions of organs, differentiation of organs, and the amount of fusion between organs are useful in distinguishing between genera but not for separating these two tribes. One exception might be the presence of a carpel ring meristem in the Gossypieae but not in the Hibisceae. Merosity of some organs may be useful in helping to distinguish between these two tribes. Bractlet merosity is four or more in Hibisceae and usually three in Gossypieae. Stamen merosity appears to be higher in the Gossypieae than in the Hibisceae. All of these characters need to be tested using many more taxa in each tribe.

Even though ontogenetically these two tribes are quite similar and they share several morphological attributes, there is quite a lot of evidence by previous researchers to keep these two tribes separate. According to Fryxell (1968, 1975, 1979), members of the Gossypieae are unique to Malvaceae and angiosperms in having gossypol glands. Other characteristic such as pollen structure (Fryxell, 1968; Christensen, 1986), embryo morphology (Fryxell, 1968), presence of involucral nectaries (Fryxell, 1968), and cytological data (Bates, 1965; Fryxell, 1968) help to distinguish the members of Gossypieae from the Hibisceae. However, according to La Duke and Doebley (1995), chloroplast DNA data may "reiterate the link between the Hibisceae and the Gossypieae and question the monophyly of the Hibisceae." In their analysis the three representatives of Gossypieae form a monophyletic group. Similarly,
A phylogenetic analysis by Fryxell and La Duke (1994) using morphological characters indicated the integrity of the Gossypieae clade and the Hibisceae intact to a lesser extent. At present, these two tribes should be considered as separate but closely allied. Hopefully a cladistic analysis using ontogenetic and morphological characters (upcoming chapter) will help to better define these tribes and add insight into the placement and hierarchical rank of the Gossypieae group in the Malvales.

*Abelmoschus* was separated from the genus *Hibiscus* on the basis of a calyx that is spathaceous, two- or three-lobed, and deciduous before the fruit matures (Kearney, 1951). Kearney (1951) also described earlier research by Skovsted (1944), which indicated the separation of these genera based on hybridization studies, and a study by Hochreutiner (1924), which dismissed the character of a spathaceous calyx as being shared by certain species of *Hibiscus*. The latter author indicated that a good generic character is the "basal cohesion of the calyx with" the petal-stamen tube so that the calyx, petals, and stamens fall off as a unit. Fryxell (1988) also reported that species of *Abelmoschus* have a spathaceous calyx that splits asymmetrically at anthesis and fall off with the corolla. Although I lacked fully mature flowers of *Abelmoschus manihot* and cannot verify the amount of fusion or the caducous nature of the sepals, the early initiation of the calyx in this species was the same as in *Hibiscus lasiocarpos*. Both taxa initiate five sepals in a simultaneous order on a low sepal ring meristem and have connate sepals. In addition, I found no evidence of ontogenetic fusion of the calyx to the petal-stamen ring meristem or subsequent adnation between the calyx and the petal-stamen tube. In general, the early ontogeny of flowers in these two taxa
is very similar. One character that does distinguish them is that in *A. manihot* the styles are fused their entire length whereas in *H. lasiocarpos* the styles separate apically. This may be considered to be a generic distinction since Fryxell (1988) typified the genus *Abelmoschus* as having a single style with 5 sessile capitate stigmas and the genus *Hibiscus* with five styles that are distally free with capitate stigmas. Another distinction between these two taxa is that in *H. lasiocarpos* the pedicels are distinctly jointed, while in *A. manihot* the pedicels are not jointed; it is unknown if this distinction can be applied to all members of these genera.

*Radyera* has several features that set it apart from the other taxa. According to Fryxell and Hashmi (1971), *R. farragei* is believed to be unique among the Malvaceae in having stipular nectaries; it is not known if this feature is also present in the other species of *Radyera*, *R. urens*. *R. farragei* is also unique in the Hibisceae in having both loculicidal and septicidal dehiscence, with the five-celled capsule dividing at maturity into ten segments; the Hibisceae typically has capsules with only loculicidal dehiscence (Fryxell and Hashmi, 1971). *Radyera* is also set apart from other malvaceous taxa (including *Hibiscus*) by some embryo characteristics, by having oblate to suboblate pollen grains that are zonicolporate with less than ten apertures. Current members of *Hibiscus* (and most of the Malvaceae) have spheroidal to spherical pollen that is panporate with many to numerous apertures. In fact, zonicolporate pollen has otherwise only been found in the Malveae. *Radyera* is also distinguished from *Hibiscus* by having an undivided style (this research, Fryxell and Hashmi, 1971). Other characters that I found in my examination of *R. farragei* that help to delineate the species (and possibly the genus) are the lack of jointed pedicels, connation of the involucellar bracts, absence of an
involucellar ring meristem, helical initiation of common bractlet primordia, absence of a calyx ring meristem, helical initiation of the sepals, lack of space left on the androecial ring meristem in front of the lagging rows of stamens, and irregularity of the androecial teeth. The combination of ontogenetic and morphological characters clearly separates *Radyera* from *Hibiscus* and may even place the genus at the periphery of the tribal limits.

**Characterization of tribes** — The following characterization of the Hibisceae and Gossypieae is preliminary. Only a limited number of taxa could be examined in this research project, and it should be noted that the Hibisceae is quite large with 53 genera (Fryxell, 1968, 1975, 1997) and that many genera in both tribes contain numerous species (Fryxell, 1968, 1988). As more taxa are examined in each tribe the boundaries for each may have to be expanded and readjusted.

Representative flowers in the Hibisceae typically have four to fourteen bractlets that may be separate or basally fused. The number of bractlets varies among taxa and may vary within species. Bractlet primordia, or in some taxa common bractlet primordia, initiate in helical sequence. Formation of a bractlet ring meristem may precede bractlet initiation in some taxa. The calyx is five-merous and basally fused. Initiation of the sepals may or may not involve a sepal ring meristem and the order of initiation can be simultaneous or helical. The corolla exceeds the calyx in length and flares distally (i.e. campanulate corolla) to form an open flower or some species (Fryxell, 1988, 1997) have tubular corollas. The five petals are not connate but are basally adnate to the androecium. Prior to petal initiation, five common petal-stamen mounds are produced on a petal-stamen ring meristem. A petal primordium initiates on the outer perimeter of each mound at about the same time as a
common stamen mound initiates on the raised surface. The order of initiation of the petals is simultaneous. The petals are positioned alternate to the sepals. The androecium consist of 40 to 160 stamens; with numbers varying among taxa and within a species. The first five common stamen mounds or regions become laterally divided to yield a whorl of ten common stamen primordia. From these ten common stamen primordia, proliferation of common stamen primordia proceeds in a centrifugal direction so that there are ten radial rows of common stamen primordia, usually five leading and five lagging radial rows. Most of the primordia in these rows will bifurcate in a lateral or oblique direction to yield two stamen primordia each. The stamen groups are basically opposite the petals. The filaments may diverge either singly or in pairs from the androecial column. Stamen filament divergence is radial and usually throughout the length of the column. At the apex of the androecial column, five sterile teeth are initiated. In some taxa the teeth may become lobed or divided at maturity. The pollen is spheroidal or rarely oblate to suboblate in shape, has numerous spines, and has either porate or colporate apertures. The gynoecium is usually shorter than the corolla. It contains five fertile carpels (rarely 10 in aberrant collections). Each locule many contain one, several, or numerous ovules depending on the species. The ovary is syncarpous, superior, and has axile placentation. The styles are fused into a column that may diverge apically in some taxa. The stigma type is capitate and there is a one to one ratio of stigmas to mericarps. Early initiation of the gynoecium does not appear to involve a carpel ring meristem. All of the carpel primordia of the gynoecium initiate simultaneously in a single whorl (except in possibly aberrant polymerous flowers). There is an apical
residuum in the center of the young gynoeicum. The fruit type is a dehiscent capsule.

The taxa representing the Gossypieae differ from the Hibisceae in several respects. Bractlet merosity is usually three, although in some taxa the bractlets may be suppressed to some degree. (Fryxell (1979) listed most genera in this tribe with three bractlets, although some taxa may have none, or many.) In the taxa I examined, no bractlet ring meristem was observed and the order of initiation of the bractlet primordia was helical. There was no connation between the bractlets. In the calyx whorl, only helical initiation was observed. The number of stamens numbered 110 to 200, with variation among taxa and within a species. The first five common stamen mounds may laterally divide to form ten or 15 common stamen primordia. Therefore, in some taxa the common stamen primordia are not always arranged in ten radial rows and there is not always a set of leading and lagging rows. Most of the stamen groups are opposite the petals, but in at least one taxon the stamen groups are alternate with the petals. The filaments diverge mostly in pairs (sometimes singly) and some of the filament pairs may be basally partially fused above the point of divergence from the androecial column. The pollen is typically spheroidal. The gynoecium consist of three to five fertile carpels with several ovules per locule. The styles are fused their entire length and may be terminated by capitate or decurrent stigma lobes. A low carpel ring meristem may be involved in carpel initiation. The fruit is a dehiscent or indehiscent capsule.

The use of floral ontogeny (with the advancement in microscopy of SEM) is a highly useful tool to elucidate similarities and differences among genera and tribes and to clarify the formation of the many unusual floral
features found in malvaceous flowers. Cladistic analysis using ontogenetic characters (future research) may help to determine evolutionary relationships among members of the Malvaceae and may support or clarify current analyses which use morphological and molecular data.

LITERATURE CITED


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FLORAL ONTOGENY AND PHYLOGENY
IN MALVACEAE

VOLUME II

A Dissertation

Submitted to the Graduate Faculty of the
Louisiana State University and
Graduate College
in partial fulfillment of the
requirements for the degree of
Doctor of Philosophy

in

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December 2000
CHAPTER 4
FLORAL DEVELOPMENT IN MALVEAE

INTRODUCTION

Malveae St.-Hilaire is one of five currently recognized tribes comprised in the plant family Malvaceae (Fryxell, 1975, 1988). It is a large tribe with approximately 72 genera (Bates and Blanchard, 1970; Fryxell and Fuertes, 1992; Fryxell, 1988). Since this is such a large tribe with a great amount of taxonomic complexity, attempts have been made to divide the taxa into various groups. Early researchers divided the Malveae into subtribes primarily on the basis of morphological characteristics (Le Maout and Decaisne, 1876; Schumann, 1891; Edlin, 1935; Kearney, 1951; Hutchinson, 1967). More recently, the tribe has been divided into alliances using not only comparative morphology, but also cytological data, and in some cases palynology (Bates, 1968; Bates and Blanchard, 1970; Bates, 1976; Fryxell, 1978, 1988; Fryxell and Fuertes, 1992). In addition, members of the former Malopeae tribe were incorporated into the Malveae by Bates (1968). According to Fryxell and Fuertes (1992), generic boundaries in this tribe have been one of the most challenging systematic problems in the Malvaceae.

The eight species (Malva neglecta, Abutilon parishii, Lavatera trimestris, Sida rhombifolia, Modiola caroliniana, Callirhoe involucrata var. involucrata, Anisodonta x hypomandarum, and Iliamna remota) chosen for this research have not been in question as far as placement in the tribe, but alliance affiliations are less certain. Malva is the type genus for the tribe. It contains over 100 species from Europe, North Africa, Asia, and some have been introduced into the Americas. The genus contains some weeds and
some ornamentals. *Abutilon* is a large genus with about 160 species and it occurs on all continents except Antarctica (Fryxell, 1988, 1997). *Lavatera* contains 20 to 23 species principally from the Mediterranean region but also indigenous to the California area (Ray, 1995; Fryxell, 1997). Some are cultivated in gardens (Fryxell, 1988, 1997). *Sida* is found in the Americas, Africa, Asia, and Australia (Fryxell, 1988). Estimates on the number of species has varied greatly, but the most recent estimate is about 100 (Fryxell, 1997). *Modiola* is a monotypic genus occurring from the United States to Argentina as well as in the Old World. It frequently occurs as a weed (Fryxell, 1988). *Callirhoe* is a small genus with nine species currently recognized from the United States and northern Mexico (Doir, 1990). *Anisodontea* is a genus confined to southern Africa (Bates, 1968, 1969). It consist of 19 species with several subspecies and one named hybrid (Bates, 1969). *Iliamna* contains seven (or eight species) from temperate North America (Wiggins, 1936; Kearney, 1951; Mohlenbrock, 1982, Fryxell, 1997).

Members of the Malvaceae are tropical to temperate trees, shrubs, or herbs. The flowers are typically solitary or fasciculate in leaf axils or grouped in inflorescences. They are usually pentamerous, polysymmetric, and bisexual with an involucel or involucre, a monadelphous androecium, and a superior gynoecium. Anthers are bisporangiate and monothechal. Fruits are schizocarps, capsules, or sometimes berries. Pollen is typically spheroidal and echinate (Fryxell, 1968, 1975, 1988; Cronquist, 1981).

The Malveae is distinguished from other Malvaceae tribes by a combination of morphological characters. Features that in combination characterize the tribe are: schizocarpous fruit with three to many mericarps, free gynoecial styles, stigma number equaling locule or mericarp number,
lack of sterile teeth at the apex of the androecial column, and lack of gossypol glands (Fryxell, 1968, 1975, 1988). The carpels may be pluriovulate or uniovulate with ovules either pendulous or ascending (Bates, 1968). Also, members of this tribe lack foliar nectaries (Fryxell, 1975, 1988) and involucellar nectaries (Fryxell, 1988).

One purpose of this project is to make a comprehensive study of floral ontogeny in the Malveae using scanning electron microscopy (SEM). Previous floral developmental studies of some members of this tribe have used light microscopy techniques. Payer (1857) looked at various stages of floral development. Saunders (1936) and Rao (1952) described the vascular system, van Heel (1966) examined the androecium, Christensen (1986) looked at pollen morphology, and Sattler (1973) looked at organogenesis of two members of this tribe. Van Heel (1995) used SEM to look at gynoecial development in two taxa. Endress (1994) also used SEM to described sporadic stages in some malvaceous taxa. None of these studies, with the exception of Sattler (1973), included a complete ontogenetic series to show floral development in a member of this tribe. Therefore, a complete ontogenetic series with the high resolution provided by SEM is needed for members of this tribe.

Another purpose of this research is to use development to analyze the many unusual structures in flowers of Malveae. One such structural anomaly found in malvaceous flowers is the fused multistaminate androecial column with a basally adnate corolla. Accounts of how the stamens and petals initiate in this family have often been incomplete, confusing, and contradictory. In one interpretation, Payer (1857) described a ring meristem on which petals and stamens form, with petals appearing prior to stamens.
He did not indicate the appearance of common petal-stamen mounds. Van Heel (1966) described a "peripheral wall" on which five sectorial regions originate and develop into "staminal buttresses." Subsequently, stamen primordia originate on these buttresses in centrifugal succession and petals initiate outward from these buttresses. In 1995, van Heel characterized two members of the Malveae with androecia that first arise as continuous zonal meristems, after which each meristem differentiates into five pairs of primary stamen meristems. Petals emerge on the outside corners of the five-sided androecial meristem. Sattler (1973) depicted two members of the Malveae as having petals that initiate as distinct primordia, with adnation to the androecial column occurring later. In Alcea rosea, he described five androecial primordia initiating first, then interprimordial growth creating an almost "girdling androecial primordium." In Malva neglecta, he portrayed the androecium appearing first as a ridge, then primordia developing. In both these taxa, Sattler described "primary" (common) stamen primordia, with subsequent proliferation occurring laterally and centrifugally. Endress (1994) briefly described the occurrence of primary androecial primordia that secondarily subdivide in Kitaibelia vitifolia. In my examinations of the Malvavisceae, Hibisceae, and Gossypieae (Chs. 2, 3), I found that petals and stamens initiate from five common petal-stamen mounds or sectorial regions on a ring meristem. In addition, the petals initiate at the same time or nearly so as the first five common stamen mounds. Since the literature is contradictory as to the possible presence of a petal-stamen ring meristem or of common petal-stamen primordia, members of the Malveae need to be examined as well. This study will try to determine the nature of the association between the origin of the corolla and the androecium and the
detailed sequences of stamen proliferation in representative taxa of the Malveae.

Another morphological objective is to examine the development of the apex of the androecial column in flowers of the Malveae. Members of this tribe are characterized as lacking sterile teeth at the apex of the androecial column, whereas members of the other four tribes of Malvaceae typically have five sterile teeth (Fryxell, 1968, 1975, 1988). How the formation of the staminal tube in the Malveae might differ from the other tribes to account for the lack of sterile teeth has not been previously addressed in detail. Is there a difference in the amount of space left on the ring meristem, in the overall shape of the ring meristem, in the relative timing of elongation of the tube, or in the position of the stamen groups? Besides answering these questions, I will try to determine if some taxa initiate the sterile teeth but suppress further development of the organs. A detailed ontogenetic series is needed to show how the androecial tube might develop with or without apical sterile appendages.

The descriptions of carpel development for many of the genera in Malvaceae vary as to whether they initiate as one discrete whorl, as two whorls, or as randomly scattered carpels (Kearney, 1951; Hutchinson, 1967; Bates, 1968; van Heel, 1978). In addition, it is unclear if carpel initiation in some taxa involves a ring meristem or common primordia. Sattler (1973) suggested the formation of a carpel "rim" in some taxa. Payer (1857) described the initiation of independent carpel primordia in a whorl in some malvaceous taxa (Hibiscus, Abelmoschus, Malva, Sphaeralcea, and Pavonia) with fusion occurring later. In Kitaibelia and Malope, he depicted a pentagonal gynoecium with proliferation of numerous carpels occurring from
five common "humps". Similarly, Endress (1981) reported that in *Kitaibelia* the early gynoecium consist of five gynoecial primordia that subdivide to make a total of about 50 secondary primordia. Van Heel (1995) detailed the gynoecium in *Kitaibelia* and *Malope* as arising as a continuous girdling meristem and that 'primary' primordia were not observed; instead, the gynoecial meristem widens as a 'pentagonal wave-line' on which the carpel primordia appear simultaneously. In the Malvavisceae, I found that the carpels initiate as two sets of five in a single "spatial whorl" and that no ring meristem is involved (Ch. 2). In representatives of the Hibisceae (possibly excluding an aberrant collection of *Abelmoschus*) and Gossypieae the carpels initiate simultaneously in a single spatial whorl. A low gynoecial ring meristem precedes carpel initiation in the Gossypieae but not in the Hibisceae. Since literature describing gynoecial development in Malvaceae is lacking or is contradictory and there is evidence that carpel development may vary among the tribes of Malvaceae, a focus of this research is to clarify how carpels initiate in members of the Malveae.

A final aspect of this paper is to characterize the Malvaceae using ontogenetic characters. This research is part of a larger study to characterize and compare the tribes of Malvaceae and to use ontogenetic characters as well as morphological characters to determine the phylogeny of the tribes and genera. Tribes of Malvaceae have changed in content over the years, depending on the researcher. Comparative floral development can elucidate systematic differences among taxa. The overall aim of this study is to use scanning electron microscopy to compare floral development in representative examples of the tribes of Malvaceae, to test the validity of current tribal assignments.
MATERIALS AND METHODS

Floral material of eight species in the Malveae was collected from various sources (Table 4.1). These taxa represent seven of the 21 currently recognized tribal alliances (Table 4.2), as established by several authorities on the family. Herbarium vouchers were made and retained by the author. Floral buds of various developmental stages were collected and fixed in formalin-acetic acid-alcohol (FAA). Prior to dissection, buds were transferred through two to four changes of 95% ethanol, then dissected in 95% ethanol. Material was dehydrated in 100% ethanol and critical point dried in a Denton DCP-1 with liquid CO2. Specimens were mounted on aluminum stubs with Avery press-on Spot-O-Glue and sputter-coated with gold-palladium in an Edwards S-150 apparatus. Micrographs were taken using a Cambridge S-260 scanning electron microscope at 15 kV and spot size 6. Kodak Tri-X (TXT 4164) sheet film was used.

Floral ontogenetic series were obtained for the eight taxa sampled, using SEM. Some late stage floral characters were obtained by examination of herbarium vouchers and FAA-ethanol preserved material with various dissecting and light microscopes. In some instances, literature was used to verify or complete mature floral descriptions. Terms pertaining to floral features found in members of the Malvaceae are defined in Chapter 2.

RESULTS

*Malva neglecta* -- Organography -- The plants are herbaceous and mostly procumbent. The small flowers are solitary or more usually, in fascicles of two to four in the leaf axils. The pedicels do not appear to be jointed. The involucel consists of three green, distinct, linear bractlets.
TABLE 4.1. Sources of Malveae plant material and voucher information for taxa examined in this floral study.

<table>
<thead>
<tr>
<th>Taxon</th>
<th>Voucher</th>
<th>Source, collector, and date</th>
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</thead>
<tbody>
<tr>
<td><em>Callirhoe involucrata</em> (Torrey &amp; Gray) A. Gray var. involucrata</td>
<td>TSC-0041</td>
<td>Wildflower near Austin and Waller Co. line, TX, US, T. Crozier, Aug., 1992</td>
</tr>
<tr>
<td><em>Modiola caroliniana</em> (Linnaeus) G. Don</td>
<td>TSC-0013</td>
<td>Weed from St. Tammany Parish, LA, US, T. Crozier, June, 1992</td>
</tr>
<tr>
<td>TABLE 4.2. Generic alliances in the Malveae.</td>
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<tr>
<td><strong>ABUTILON</strong></td>
<td><strong>HERISSANTIA</strong>*</td>
<td><strong>PHYMOSIA</strong>*</td>
</tr>
<tr>
<td>Abutilon</td>
<td>Herissantia</td>
<td>(MALACOTHAMNUS)</td>
</tr>
<tr>
<td>Abutilothamnus</td>
<td></td>
<td>iliamna</td>
</tr>
<tr>
<td>Allowissadula *</td>
<td>HOWITTIA****</td>
<td>Phymosia</td>
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<tr>
<td>Bastardia</td>
<td>Howittia</td>
<td>Malacothamnus</td>
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<tr>
<td>Bastardiastrum*</td>
<td></td>
<td>Neobrittonia*</td>
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<tr>
<td>Bastardiopsis</td>
<td>KEARNEIMALVASTRUM</td>
<td>ROBINSONELLA*</td>
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<tr>
<td>Billietumera*</td>
<td>Kearneimalvastrum</td>
<td>Robinsonella</td>
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<tr>
<td>Corynabutilon</td>
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<td>Hochreutinera*</td>
<td>NAPAEA</td>
<td>SIDALCEA</td>
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<tr>
<td>Neobaclea</td>
<td>Napaea</td>
<td>Sidalcea</td>
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<td>Pseudoabutilon</td>
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<td><strong>ANISODONTEA</strong></td>
<td><strong>MALVA</strong></td>
<td>SPHAERALCEA</td>
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<tr>
<td>Anisodontea</td>
<td>Alcea*</td>
<td>Acaulimalva*</td>
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<td></td>
<td>Althaea</td>
<td>Calycuognygas</td>
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<td></td>
<td>Lavatera*</td>
<td>Calytraemalva</td>
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<td><strong>MOBIOLA</strong>*</td>
<td>SIDA*</td>
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<td>Briqueia</td>
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<td>Dendrosida</td>
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<td>Dirhamphis</td>
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<td>Krapovickiasia</td>
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<tr>
<td><strong>FRYXELLIA</strong>*</td>
<td><strong>ASTEROTRICHION</strong></td>
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<td>Fryxellia</td>
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<td><strong>PLAGIANTHUS</strong></td>
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<td>Cristaria</td>
<td>Plagianthus</td>
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<td>Sidastrum</td>
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<td></td>
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<td>Tetrasida</td>
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This table is based primarily on data from Bates (1968) and Bates and Blanchard (1970), but some changes have been made to favor more recent taxonomic treatments by Fryxell (1978, 1988, 1996, 1997) and Fryxell and Fuertes (1992). Addition of new alliances or new taxa to an existing alliance are indicated *. Notes: ** Bates and Blanchard (1970) placed Callirhoe in its own alliance, but Fryxell (1988) includes it in Sidalcea alliance. *** The name of this alliance appears to have changed, but iliamna was not accounted for in the change. **** Howittia was placed in the Hibisceae by Fryxell (1968) and some treatments question whether it should be in Malvaceae.

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The five-lobed calyx is green and exceeds the bractlets in length. The five-merous corolla is white or very light pink to pale lavender and spreads distally to form an open flower. Each petal is apically notched. The androecium is included and is antheriferous only at the upper portion. The gynoecium is terminated by 12 to 15 introrsely decurrent stigmas. The fruits are indehiscent schizocarps with one seed per mericarp. The sepals and bractlets persist in the fruit (observations of collected material; Radford, Ahles, and Bell, 1987; Correll and Johnston, 1979; Fryxell, 1988).

Initiation and early development of the involucel and calyx -- Usually several floral buds initiate sequentially in the axil of a leaf and stipule pair (Fig. 4.1). As the tissue beneath each floral apex elongates to form a flower stalk, three bractlet primordia initiate in helical order on the periphery of the floral apex (Figs. 4.1, 4.2, 4.5). The bractlet primordia initiate independently; no ring meristem is involved. The bractlets elongate and temporarily arch over the remaining floral apex (Figs. 4.4, 4.6). The pre-sepal apex is convex and sepal initiation begins after all of the bractlets have initiated (Figs. 4.2, 4.3). Sepal primordia initiate in a helical sequence without a sepal ring meristem (Figs. 4.3 - 4.5). As the sepals enlarge, they arch inward to temporarily cover the interior floral organs (Fig. 4.6) and with further development they are basally fused (Fig. 4.13).

Initiation and early development of the corolla and the androecium -- The apex to the interior of the sepals is initially convex and circular in outline (Fig. 4.4), but as the sepals develop it becomes flatter and pentagonal in outline (Fig. 4.5). Then a low petal-stamen ring meristem develops interior to the sepals. This ring meristem is evident by a central depression with a raised outer rim on the pre-petal apex. Concurrently with the formation of the
ring meristem, five common mounds or regions appear on the ring meristem in positions alternate with the sepals (Fig. 4.7). As the floral apex enlarges, the ring meristem and the five mounded areas on the ring meristem become more pronounced (Fig. 4.8). Then, the upper surface of each of the five common mounds develops a radial groove and becomes laterally partitioned into two common stamen primordia (Fig. 4.9). Subsequent partitioning in a centrifugal direction creates two more common stamen primordia in each sectorial region on the ring meristem (Fig. 4.10). These new common primordia are on the same radii as the first set of common primordia (Fig. 4.10). With this type of partitioning of the ring meristem, it is difficult to tell if the original five mounds divided to yield the common stamen primordia or if each common stamen primordium arose independently in its respective mounded region. Five of the radial rows (the leading rows) of common stamen primordia are more interior on the ring meristem than the five alternating rows (the lagging rows). There is a small amount of space remaining on the interior rim of the ring meristem in front of each of the lagging rows (Figs. 4.20, 4.11). Petal initiation is not apparent until after partitioning of the stamen portion of the ring meristem is well underway. The petal primordia initiate very low on the outer flank of the petal-stamen ring meristem; one petal initiates on the outer surface of each of the original five mounded areas (Fig. 4.11). This positions the petal primordia alternate to the sepals and in radial line with their associated stamen groups. The order of initiation in the petal whorl is simultaneous. After or at the same time the petal primordia are discernible, five more staminal primordia initiate centrifugally, one in each of the leading radial stamen rows and thus one per sectorial region of the ring meristem (Fig. 4.12). All of the common stamen
primordia broaden to become elliptic in shape (Figs. 4.11, 4.12), then peanut-shaped and somewhat stalked (Figs. 4.12 - 4.14), and finally each bifurcates into two stamen primordia (Fig. 4.15). Generally this process of bifurcation begins with the first-formed common stamen primordia and progresses centrifugally until all of the common stamen primordia are divided. The direction of bifurcation of the more interior common primordia is radial to oblique but the direction for the outer common primordia may be more lateral to oblique (Figs. 4.12 - 4.14). It is unclear if the last-formed staminal primordia (labeled number 3) are common primordia that undergo bifurcation or if they are discrete stamen primordia (Fig. 4.14). With the elongation of the tissue below the peanut-shaped common primordia, the stamen primordia that result from bifurcation basally share a common stalk or filament (Figs. 4.15, 4.16). As the petal-stamen ring meristem begins to elongate vertically into a short column, differentiation of the anthers (apparent by enlargement of the distal portion of each stamen primordium and the formation of an indentation between the two microsporangial regions) occurs (Figs. 4.15 - 4.17). At this time, the apex of the young androecial tube is surmounted by stamens; there is no evidence of sterile teeth (Fig. 4.16). The petal primordia become laterally broad and blade-like (Fig. 4.17), but elongation is delayed until after differentiation of the anthers. As the petals elongate, they form a contorted corolla (Fig. 4.23) that is adnate (Fig. 4.24) to the base of the androecium.

Initiation and early development of the gynoecium — The 12 to 15 carpel primordia initiate sometime after all of the common stamen primordia have initiated and the petal-stamen ring meristem has started to elongate vertically. The gynoecium appears as a ring of connate carpel primordia to
the interior of the androecial column (Fig. 4.16). It is not known if a carpel ring meristem forms prior to carpel initiation. Since all of the early carpel primordia are equal in size and spacing, it is presumed that the order of initiation is simultaneous. A large apical residuum remains to the interior of the gynoecial whorl (Fig. 4.16). All of the carpel primordia develop adaxial indentations (Fig. 4.16), then invaginations (Fig. 4.18), and then locules. One ovule initiates in each carpel locule (Fig. 4.19). At this time, the apical residuum is convex and the outer surface of the ovary has a bulge for each gynoecial member (Figs. 4.19, 4.20). After the ovules have initiated, the apical portions of the carpel primordia elongate inwardly and upwardly (Fig. 4.20) to form styles that are apically free but basally fused into a column above the ovary (Figs. 4.21, 4.22). A decurrent stigmatic surface develops on the inwardly facing side of the upper free portion of each style (Figs. 4.22, 4.24). This differentiation of the stigmas begins before the styles surpass the androecial column in height.

**Late stage and mature reproductive characters** -- The involucellar bracts remain distinct and immediately subtend the calyx. The mature sepals are basally fused about half their length. The calyx exceeds the involucel in length. Glandular trichomes are found at the inner surface of the sepal bases (Fig. 4.24). The petals remain distinct from each other but are ontogenetically fused to the base of the androecium (Fig. 4.24). Each petal develops ciliate tufts on either side of the claw (Fig. 4.23). They lack auricles, are apically notched, are double to triple the length of the sepals, and spread distally at anthesis.

In the androecium, the filaments typically diverge in pairs that are basally fused above the point of divergence from the androecial column.
Figs. 4.1 - 4.6. *Malva neglecta*, initiation of involucel, calyx, and petal-stamen ring meristem. Bars = 100 μm. 4.1. Floral shoot. On the left of the micrograph, three floral apices (A) are subtended by a leaf (L) and stipule pair (sp). The floral buds to the upper left and lower right each have three helically initiated bractlet primordia on the floral apex (the sequence of bractlet initiation is shown with numbers, with one being the first-initiated primordium). There is no evidence of a bractlet ring meristem. The shoot apex (SA) is present. 4.2. Floral apex with three bractlet primordia (sequence of initiation shown with numbers). The pre-sepal apex is convex. 4.3. Flower with three bractlet primordia (Bt). Three sepal primordia have initiated in a helical sequence (the oldest is numbered 1 and the other two are indicated with arrows). No sepal ring meristem is present. 4.4. Five helically initiated sepal primordia are indicated with numbers. The remaining floral apex is convex and circular in outline. The bractlets arch over the remaining floral apex. 4.5. The smaller bud (upper right) has three bractlet primordia and one sepal primordium (S). The larger flower has all five sepal primordia (numbered) and the remaining floral apex has flattened and is pentagonal in outline. 4.6. The sepal have elongated and arch inward to form a protective dome. The bractlets, which typically arch over the calyx, have been broken off and lie adjacent to the bud.
Figs. 4.7 - 4.12. *Malva neglecta*, initiation of petals and stamens. Bars = 100 μm. 4.7. A petal-stamen ring meristem with five common mounds (m) alternate to the sepals. 4.8. The petal-stamen ring meristem has enlarged laterally and vertically. Each of the five mounds or regions has a barely defined radial groove. 4.9. The ring meristem is partitioned into ten common stamen primordia or mounds, two in each region (common stamen primordia in one sectorial region are numbered with 1s). 4.10. Centrifugal initiation of more common stamen primordia (numbered with 2s in one region) in radial line with the first five common stamen primordia. Five of the radial rows (the leading rows) are more interior on the ring meristem than the other five alternating rows (the lagging rows). Five small spaces (R, only one labeled) remain on the ring meristem interior to the lagging stamen rows. Petal primordia are not present. 4.11. Petal primordia (P) have initiated simultaneously on the lower peripheral flank of the the petal-stamen ring meristem. The common stamen primordia on the inner surface of the ring meristem have elongated in a radial or oblique direction. 4.12. Centrifugal initiation of five more common stamen primordia (numbered 3). The oldest common stamen primordia (numbered 1) are peanut-shaped and the next formed primordia (number 2) have broadened and are elliptic in shape (only one region labeled). A petal primordium is present at the base of each region of the ring meristem.
Figs. 4.13 - 4.18. *Malva neglecta*, androecial development and initiation of the gynoecium. Bars = 100 μm. 4.13. Most of the common stamen primordia have broadened and are elliptic, two-lobed, or peanut-shaped. Petal primordia are present. The sepals are basally fused. 4.14. The ring meristem has elongated vertically into a short tube. The oldest common stamen primordia are partially bifurcated (the products of the bifurcations for one region are indicated with prime numbers). 4.15. Common stamen primordia have bifurcated, and the stamen primordia (St) have broadened apically. The paired stamens that resulted from bifurcation share a common filament (at arrows). 4.16. Partial androecial tube (Ad) with stamens that are partially differentiated into anthers (a) and filaments (f). A whorl of connate carpel primordia (C, only one labeled) has initiated interior to the androecium. Each carpel primordium has a small adaxial indentation. An apical residuum (r) remains interior to the gynoecial whorl. 4.17. Young androecial column with differentiated anthers. The petals have broadened laterally and are blade-like, but vertical elongation has been retarded. 4.18. Nearly polar view of gynoecium. Each carpel (only one labeled) has an adaxial invagination (at arrow). The apical residuum is slightly convex.
Figs. 4.19 - 4.22. *Malva neglecta*, differentiation of the gynoecium. Bars = 100 μm in 4.19 and 4.20, = 500 μm in 4.21 and 4.22. 4.19. Partially dissected gynoecium to reveal that one ovule (O) has initiated in each locule. The apical residuum is convex. 4.20. Fused whorl of carpel primordia. The outer surface of the gynoecium is lobed. 4.21. Gynoecium inside a partial androecial column. The stamen diverge from the androecial column in basally fused pairs. The apex of the androecial column bears stamens, and lacks sterile teeth. The apical portion of each carpel has elongated into a short style (si, only one labeled). The styles are basally connate and apically free. The ovary (V) is segmented. Petals are basally adnate to the androecium. 4.22. Pistil with fused stylar column that separates apically into free styles with decurrent stigmas (sm). There is marked external separation of the ovary parts from each other and from the base of the stylar column.
Figs. 4.23 - 4.27. *Malva neglecta*, development of the petals and androecium, mature floral characteristics, and fruit. Bars = 1 mm in 4.23 - 4.25, = 50 μm in 4.26, = 2 mm in 4.27. 4.23. Contorted corolla prior to anthesis. 4.24. Each petal base has ciliate tufts on either side of the claw. Androecial column with differentiated bisporangiate anthers. The suture between the sporangia of each anther have pulled slightly open. Petal scars indicate adnation of the corolla to the androecium. Glandular trichomes are present on the upper surface of the sepal bases (at arrow). The stigmas are exserted beyond the androecium. 4.25. Mature androecial and gynoecial columns. The androecial column has elongated basally so that the stamens diverge from the upper half. The anthers have dehisced by longitudinal slits at the sutures between the sporangia. Most filaments diverge in pairs. The styles exceed the androecium in height, are apically free, and bear decurrent stigmas. The ovary has been dissected to reveal ovules. 4.26. Pollen grains adhere to decurrent stigmatic surface. The pollen is spheroidal or spherical, polyporate, and covered with numerous small spines. 4.27. Mature schizocarp with obvious segmentation into mericarps. Bractlets and sepals subtend the fruit.
The apex of the androecial tube is occupied by filaments with attached anthers; there is no evidence of sterile teeth (Figs. 4.21, 4.25). The external suture between the two sporangia of each anther begins to pull apart or break down even before the androecial tube has elongated completely and before the flower has fully expanded and opened (Fig. 4.24). The androecium usually has 40 or more stamens. At maturity, the stamens diverge radially from the upper half of the androecial column and the bisporangiate anthers dehisce by longitudinal slits at the external sutures between the sporangia (Fig. 4.25). The androecium is approximately half the length of the corolla.

The ovary proceeds from having lobes marking each carpel member (Fig. 4.20) to having segmentation between the developing mericarps (Figs. 4.21, 4.22, 4.25). The mature gynoecium slightly exceeds the androecium in height and each of the long slender styles bears an introrsely decurrent stigma (Figs. 4.25, 4.26). The pollen grains are spheroidal (or spherical), polyporate, and are covered with numerous short spines (Fig. 4.26). The flower symmetry is actinomorphic. The mature fruit is wider than tall and has easily discernible mericarps arranged in a ring around a central disk. The one-seeded mericarps lack endoglossa. The sepals and bractlets persist in the schizocarp (Fig. 4.27).

*Sida rhombifolia* -- Organography -- The plants are erect subshrubs with flowers solitary in leaf axils. The flowers have long jointed pedicels and lack involucels. The green calyx is apically five-lobed and basally ten-ribbed. The five-merous corolla is yellow or yellow-orange and spread distally to form an open flower. The androecium is included. The long filaments diverge only from the apical portion of the androecial column.
The gynoecium is terminated by nine to 14 styles with capitate stigmas. The fruits are indehiscent schizocarps with one seed per mericarp. The sepals persist in the fruit (observation of collected material; Fryxell, 1988).

Initiation and early development of the calyx -- A floral apex initiates in the axil of a leaf and stipule pair. Elongation of the tissue below the apex creates a stalked floral apex. (Fig. 4.28). Prior to sepal initiation, the apex is convex and often irregular in outline due to appression by the subtending leaf (Fig. 4.28). The calyx initiates as a ring meristem around the perimeter of the floral apex (Fig. 4.29). Then five sepal primordia initiate in helical sequence on the sepal ring meristem (Fig. 4.30). As the sepals elongate, they are fused basally and arch distally over the remaining floral apex to form a protective dome (Fig. 4.31). At this stage, the base of the calyx is ten-ribbed, with a rib at the midsection of each sepal base and at the fused intersection of two adjacent sepal bases (Figs. 4.31, 4.32).

Initiation and early development of the corolla and the androecium -- The apex inside the sepal ring meristem is initially pentagonal in outline and slightly convex (Fig. 4.29). After the sepal primordia have initiated, a circular depression develops between the convex center and the mounded periphery of the apex. In addition, five common petal-stamen mounds initiate in the corners of the pentagonal apex (Fig. 4.32). These common mounded areas or sectorial regions are alternate to the sepals. Next, the raised portion of the ring meristem becomes partitioned into 10 common stamen mounds (Fig. 4.33). Similar to Malva neglecta, in Sida rhombifolia a lateral pair of the common stamen primordia results from the partitioning of each of the five original common petal-stamen mounds. However, in S. rhombifolia the position of the associated pair of common stamen primordia is different in that
one member is in the corner of the pentagonal ring meristem (alternate to the
sepals) and the other is oriented along the side of the pentagonal ring
meristem (in a position slightly off-center but on the radii of the sepals) (Fig.
4.34). Petals initiate after the ten common stamen primordia are present.
The petal primordia initiate very low on the outer flank of the petal-stamen
ring meristem; one petal initiates on the outer basal surface of each of the
original five mounded areas or sectorial regions (Fig. 4.34). The petals are
alternate to the sepals and initiate in a simultaneous order. With elongation
of the ring meristem into a short tube, five small spaces form on the inner
surface of the tube (Fig. 4.35). One to three additional staminal primordia
may initiate centrifugally outside the set of ten common stamen primordia;
they generally do not initiate as a complete set of five or some multiple of five
(Figs. 4.36 - 4.38). If these extra-staminal primordia initiate, each is in a
position interior and alternate to the petals (Figs. 4.36 - 4.38). All of the
common stamen primordia broaden to become elliptic (Figs. 4.35, 4.36), then
peanut-shaped (Figs. 4.37, 4.38), and then bifurcate into two stamen
primordia each (Fig. 4.39). The direction of bifurcation in obliquely radial to
obliquely lateral (Fig. 4.38). Members of the second set of staminal primordia
may broaden and even become two-lobed (Fig. 4.38), but it is uncertain if
these primordia bifurcate to yield two stamens, develop into single stamens,
or abort. The tissue below the peanut-shaped common primordia elongates
so that stamen primordia that result from bifurcation share a common stalk or
filament at the base (Figs. 4.42, 4.45). As the petal-stamen ring meristem
elongates vertically into a column, the bisporangiate anthers differentiate
(Figs. 4.39 - 4.41). At this time, the androecial column is surmounted by
stamens; there is no evidence of sterile teeth (Fig. 4.45). Petal growth is
retarded until after the anthers have developed (Figs. 4.41, 4.45). The corolla is basally adnate to the androecium (Fig. 4.45).

**Initiation and early development of the gynoecium** -- The pre-carpel apex is initially flat (Figs. 4.34, 4.35), and then becomes slightly convex (Figs. 4.36, 4.42). The nine to 14 carpels initiate after all of the common stamen primordia have initiated. The gynoecium appears as a ring of connate carpel primordia to the interior of the androecium (Fig. 4.43). The carpel primordia initiate simultaneously. It is not known if a carpel ring meristem precedes initiation of the primordia. An apical residuum remains to the interior of the gynoecial whorl (Fig. 4.43). As each carpel primordium invaginates and forms a crevice, a small lobe of tissue develops adaxial to each carpel crevice (Fig. 4.44). The lower portion of the carpels expands and elongates to form a syncarpous ovary (Fig. 4.45). After ovules have initiated, the apical portion of each carpel elongates to form a style (Fig. 4.46). As elongation of the gynoecial members continues, the styles fuse just above the ovary, but for most of their length they remain separate. For a time, the styles elongate more rapidly than the androecial column and the petals so that the styles temporarily surpass the latter in height and can be found curling downward among the anthers in immature flower buds (Figs. 4.47, 4.48). Each style develops a capitate stigma (Figs. 4.47 - 4.49).

**Late stage and mature reproductive characters** -- The mature sepals are fused about 3/4 their length. Glandular trichomes are found at the inner surface of the sepal bases (Fig. 4.50). The petals remain distinct from each other but are fused to the base of the androecium. Each petal base has ciliate tufts on the sides of the claw. The petals are apically asymmetrical, slightly exceed the calyx in length, and spread distally to form an open flower.
Figs. 4.28 - 4.33. *Sida rhombifolia*, initiation of sepals, petal-stamen ring meristem, and common mounds. Bars = 50 μm. 4.28. Stalked floral apex in axil of leaf and stipule pair. The floral apex is convex and irregular in outline due to appression by the leaf. 4.29. Sepal ring meristem. The pre-petal apex is pentagonal in outline. 4.30. Five sepal primordia. The sepals initiate in helical sequence (possible sequence of initiation shown with numbers). The pre-petal apex is convex. 4.31. The sepals are fused basally and arch over the remaining floral apex. The lower outer surface of the calyx is ten-ribbed, with a rib at the basal midsection of each sepal and at the intersection of adjacent sepals. 4.32. A shallow depression separates the convex center of the pre-petal apex from the mounded periphery. Five common petal-stamen mounds at the corners of the pentagonal apex. These mounds are interior and alternate to the sepals. The basal portion of the calyx is ten-ribbed. 4.33. A petal-stamen ring meristem with ten apical mounds (only two labeled). (The left side of the ring meristem is damaged).
Figs. 4.34 - 4.39. *Sida rhombifolia*, initiation of petal and stamen primordia. Bars = 100 μm. 4.34. Ten common stamen primordia are present on a petal-stamen ring meristem. The paired common primordia in one region are labeled with number 1s. Each associated pair of common stamen primordia has one member positioned in the corner and the other member oriented along the side of the pentagonal ring meristem. Five petal primordia have initiated simultaneously at the abaxial base of the ring meristem; one petal primordium is situated in each of the five regions of the ring meristem. The petal primordia are alternate to the sepals. The pre-carpel apex is flat. 4.35. The ring meristem has elongated and five small spaces (R, only one labeled) are present on the interior surface of the ring meristem. Each of the ten common stamen primordia has broadened in an oblique direction. 4.36. Three additional staminal primordia (numbered 2) have initiated centrifugally, in addition to the original ten common stamen primordia. The first ten common stamen primordia have broadened to an elliptic shape. The pre-carpel apex is convex. 4.37. The first ten common stamen primordia are each two-lobed. Two additional staminal primordia are present (numbered 2). 4.38. All the first ten common stamen primordia are peanut-shaped. Three additional staminal primordia are present in a second set; two of these are two-lobed. 4.39. Each of the common stamen primordia has bifurcated to yield two stamen primordia.
Figs. 4.40 - 4.45. *Sida rhombifolia*, development of the androecium and initiation and early development of the gynoecium. Bars = 200 μm in 4.40, 4.41, and 4.45, = 50 μm in 4.42 - 4.44. 4.40. Androecium elongated into a short column. The anthers are in the early stages of differentiation. The petals have broadened and are growing marginally, but they have not elongated significantly. 4.41. Further elongation of the androecial column. Petal elongation has been retarded. Petals are adnate to the base of the androecium. 4.42. Mounded pre-carpel apex. Small spaces remain on the interior surface of the androecial ring meristem. 4.43. A continuous ring of carpel primordia which initiated simultaneously. 4.44. A whorl of nine carpel primordia. All of the carpel primordia have crevices. A small lobe of tissue has developed between each carpel crevice and the remaining floral apex. 4.45. Androecial column that has been partially dissected. The apex of the androecial tube lacks sterile teeth. The filaments are basally fused into pairs. The petals are basally adnate to the androecium. The young gynoecium has basally fused carpels forming a syncarpous ovary.
Figs. 4.46 - 4.52. *Sida rhombifolia*, gynoecial development and mid and late stage floral characteristics. Bars = 250 μm in 4.46, = 500 μm in 4.47, 4.48, 4.50, and 4.51, = 100 μm in 4.49, = 2 mm in 4.52. 4.46. Gynoecial whorl and androecium partly dissected. The apical portion of each carpel has elongated. 4.47. Petals have elongated and are forming a contort corolla. The styles with stigmas have elongated and curl downward among the anthers. 4.48. Partially dissected androecium and gynoecium. Each locule contains one ovule with an apical appendage. The seam between the sporangia of each anther has deepened. Each style has a capitate stigma. 4.49. Capitate stigma with pollen grains. Pollen is spheroidal and echinate. 4.50. Mature androecial and gynoecial columns. The anthers have dehisced at longitudinal slits between the sporangia. All of the filaments diverge from the apical portion of the androecial column. Each ovule has an apical appendage and each segment of the ovary has two apical appendages (at arrows). Glandular trichomes are found at the inner surface of the sepal bases (N). 4.51. Immature fruit. Each mericarp (M) has two apical appendages pointing upward and inward towards the center of the fruit. 4.52. The mature fruit is broader than tall and has persistent sepals. The apical appendages meet as a small mound in the center of the fruit.
In the androecium, the filaments typically diverge in pairs from the apical portion of the column (Fig. 4.50). Stamen number is usually 20 to 30 and the anthers are bisporangiate. There are no sterile teeth at the apex of the androecium. Anthers dehisce by longitudinal slits at the external suture between the two sporangia (Fig. 4.50). The androecium is 1/4 to 1/2 the length of the corolla.

At maturity, the exserted portion of the styles and stigmas curl downward among the anthers (Fig. 4.50). The stigmas are capitate (Fig. 4.49). Each locule contains one ovule (Figs. 4.48, 4.50). Apical appendages develop external to the style bases on the upper surface of the ovary. All of these appendages point inward and upward toward the center of the gynoecium and there are two appendages per mericarp (Figs. 4.50, 4.51). The pollen grains are spheroidal and spiny (Fig. 4.49). The mature fruit is broader than tall, lacks endoglossa in the mericarps, has persistent sepals which radiate upward, and has a whorl of pointed appendages that meet at the apical center of the fruit (Fig. 4.52).

**Modiola caroliniana** — *Organography* — The plants are perennial, trailing herbs with flowers solitary in leaf axils. The pedicels are not jointed. The involucel consist of three green, distinct, foliaceous bractlets. The calyx is five-lobed, green, and exceeds the involucel in length. The five-merous corolla is orange to maroon in color with a darker base and spreads distally to form a small open flower. The androecium is included and is antheriferous only at the upper portion. The gynoecium is terminated by 15 to 25 capitate stigmas. The schizocarp may be indehiscent or dehiscent, contains two seeds per mericarp, and has persistent sepals and bractlets.
(observations of collected material; Correll and Johnston, 1979; Radford, Ahles, and Bell, 1987; Fryxell, 1988).

Initiation and early development of the involucel and calyx — A floral bud initiates in the axil of a leaf and stipule pair (Figs. 4.53, 4.54). The three bractlet primordia initiate in helical sequence on the periphery of the floral apex (Figs. 4.53, 4.54). The bractlet primordia initiate independently; no ring meristem is involved. The pre-sepal apex is convex and the sepals initiate after all of the bractlet primordia have initiated. A low, poorly defined sepal ring meristem develops concurrently with initiation of the first sepal primordium (Fig. 4.55). Five sepal primordia initiate in a helical succession (Fig. 4.56). The bractlets elongate and broaden to become leaf-like. As the sepal enlarge, they arch inward to cover the remaining floral apex (Figs. 4.57 - 4.59) and with further development they are basally fused (Fig. 4.63).

Initiation and early development of the corolla and the androecium — The apex to the interior of the sepals is initially convex and nearly pentagonal in outline (Fig. 4.56). Then five mounded areas develop in positions alternate to the sepals (Fig. 4.57). With further development, a raised rim develops where the five mounds are located and a depression develops in the center of the remaining floral apex, thus indicating the formation of the petal-stamen ring meristem (Fig. 4.58). As the ring meristem enlarges, the original five alternisepalous mounds become indistinct on the low ring meristem and five laterally broad common stamen primordia initiate in positions opposite the sepals (Fig. 4.60). Each of these five common stamen primordia becomes two-lobed, giving a total of ten (Figs. 4.61, 4.62). Generally five more common stamen primordia develop centrifugally on the androecial ring meristem; the number and position of these is variable.
Typically, this second set of common stamen primordia are initiated centrifugally and off-center to the first five common stamen primordia (Figs. 4.62, 4.63). The five petal primordia initiate at about the same time as the second set of common stamen primordia. The order of initiation among the petals is simultaneous. Petal primordia initiate very low on the outer flank of the androecial ring meristem in positions alternate to the sepals and to the stamen groups (Figs. 4.62, 4.63). All of the common stamen primordia become peanut-shaped, then laterally bifurcate to yield two stamen primordia each (Fig. 4.64). Before bifurcation of the common stamen primordia, there are spaces left on the ring meristem between the primordia (Fig. 4.63). As the petal-stamen ring meristem begins to elongate vertically into a column, differentiation of the anthers occurs (Figs. 4.64, 4.65). The young androecial tube is surmounted by stamens, and there is no evidence of sterile teeth (Figs. 4.64, 4.65). Petal primordia become laterally broad by marginal growth, but elongation is delayed until after differentiation of the stamens and initiation of locules in the gynoecium (Figs. 4.65, 4.69, 4.70).

Initiation and early development of the gynoecium — The pre-carpel apex proceeds from being relatively flat (Fig. 4.61) to slightly convex (Fig. 4.62). Then a low ring meristem develops with the outer rim slightly raised around a central depression (Fig. 4.66). This differentiation of the carpel ring meristem occurs at the time the anthers are starting to form-differentiate. Fifteen to 25 carpel primordia initiate simultaneously on the low ring meristem (Figs. 4.64, 4.67). An apical residuum remains to the interior of the carpel primordia (Figs. 4.67-4.70). Each carpel primordium develops a small adaxial indentation (Figs. 4.67, 4.68), then crevices (Figs. 4.69 - 4.71), and then locules (Figs. 4.72, 4.73). Two ovules develop in each locule (Figs.
4.72, 4.73). The apical portion of each carpel elongates inward and upward to form a hollow stylar column that is fused basally above the ovary but separate apically (Figs. 4.72 - 4.74). The surface of the syncarpous ovary develops the same number of lobes as the number of locules (Figs. 4.73, 4.75). Each style develops a capitate stigmatic surface at about the time it elongates beyond the androecial column (Figs. 4.74, 4.75).

**Late stage and mature reproductive characters** -- The involucellar bracts remain distinct and immediately subtend the calyx. The calyx exceeds the involucel in height. The mature sepals are fused less than half their length. Glandular trichomes are found on the inner surface of the sepal bases (Fig. 4.75). The petals are ontogenetically fused to the base of the androecium (Figs. 4.71, 4.75). As the petals elongate, they form a contorted corolla (Figs. 4.74, 4.76). Each petal has ciliate tufts on the sides of the claw (Fig. 4.75). The mature petals exceed slightly the calyx in height and they spread distally to form a small open flower.

In the androecium, the filaments diverge in pairs or singly from the apical portion of the elongated column. There is no evidence of sterile teeth. The anthers dehisce by longitudinal slits between the sporangia. Stamen number is usually between 15 and 20, but others report the range between 10 and 30 (Correll and Johnston, 1979; Radford, Ahles, and Bell, 1987). The androecial column is only about half or less the length of the corolla.

The ovary develops numerous trichomes (Fig. 4.75) which get quite long as the flower reaches anthesis. Even late in floral development the apical residuum persists so that the stylar column is hollow (Fig. 4.74). At maturity, however, the stylar column becomes solid, but there is a small hollow space in the ovary in the location of the apical residuum. The mature
Figs. 4.53 - 4.58. *Modiola caroliniana*, initiation of bractlets, sepals, common mounds, and petal-stamen ring meristem. Bar = 100 μm. 4.53. Floral apex with one bractlet primordium. 4.54. Floral apex in axil of leaf and stipule pair. Three bractlet primordia have initiated helically (sequence of initiation shown with numbers). 4.55. Low sepal ring meristem (at arrows) and one sepal primordium. 4.56. Sepal ring meristem with five sepal primordia (sequence of initiation shown with numbers). 4.57. Five sepal primordia. The pre-petal apex has five mounded areas in positions alternate to the sepals. 4.58. Early formation of petal-stamen ring meristem is indicated by depression in the center of the floral apex. Five mounded areas are present on the ring meristem.
Figs. 4.59 - 4.62. *Modiola caroliniana*, development of sepals, proliferation of stamens, and initiation of petals. Bars = 100 μm. 4.59. The sepals have elongated, are fused basally, and arch apically over and protect the interior floral organs. No connation has occurred among the bractlets. 4.60. Common petal-stamen ring meristem. The initial five common mounds are not apparent. The ring meristem has five common stamen primordia (numbered 1) oriented opposite the sepal scars; these stamen primordia are each broad laterally with a shallow radial indentation. 4.61. The first five common stamen primordia are broad laterally and two-lobed. These common stamen primordia are opposite to the sepals. 4.62. A second set of common stamen primordia has initiated in an oblique centrifugal direction. Usually five secondary primordia initiate, but in this flower bud there are some aberrations. The first common stamen primordia are peanut-shaped. Petal primordia have initiated simultaneously in positions alternate to the sepals and to the stamen groups.
Figs. 4.63 - 4.68. *Modiola caroliniana*, development of the androecial column and initiation and development of carpels. Bars = 100 μm. **4.63**. The first five common stamen primordia have bifurcated and each of the second set have become two-lobed. Spaces remain on the androecial ring meristem (R, only one labeled). The continuous sepal scar indicates the basal fusion of the calyx members. **4.64**. Most of the common stamen primordia have bifurcated. Some additional stamen primordia are present. Petal elongation has been delayed. Carpel primordia have initiated and small adaxial indentations are present in each carpel primordium. **4.65**. The anthers have partially form-differentiated and the androecial ring meristem has elongated into a short tube. Petals are adnate to the base of the androecium. Elongation of the petals has been retarded. **4.66**. The pre-carpel apex has a center depression and a low peripheral ridge indicating the initiation of a poorly defined carpel ring meristem. **4.67**. A connate ring of 17 carpel primordia. Each primordium has a small adaxial indentation. **4.68**. Slightly older gynoecium with a deeper indentation in each carpel primordium. A large flat apical residuum remains to the interior of the carpels.
Figs. 4.69 - 4.72. *Modiola caroliniana*, gynoecial development. Bars = 200 μm. 4.69. Partial androecial tube with a young gynoecium. The filaments and anthers diverge from the apex of the column; no sterile teeth are present. Each carpel has elongated slightly and has an adaxial crevice. The apical residuum is concave. 4.70. Further elongation of the gynoecium and deepening of the locular crevices. The apical residuum is more concave. The filaments diverge singly or in pairs from the young androecium. 4.71. Polar view of gynoecium within the base of the androecium. Each carpel has a deep narrow locular crevice. Petals are adnate to the androecial base and have broadened. The base of the calyx is connate. 4.72. Partially dissected gynoecium. Each locule contains two ovules. The apical portion of each carpel has elongated into a short, partially fused column. The apical residuum still persists.
Figs. 4.73 - 4.76. *Modiola caroliniana*, mid and late stage floral development. Bars = 500 μm. 4.73. Gynoecial column with partially dissected ovary. The ovary surface is lobed in accordance with the number of carpels. Each locule has two ovules. The styles are fused basally and the apical portions have broadened. 4.74. Longitudinal section of immature flower. Stigmatic surfaces have started to develop at the tips of the styles. Petals have elongated and overlap. 4.75. Androecium with petals removed. The styles have capitate stigmas and the ovary is segmented and covered with immature trichomes. 4.76. Nearly mature contort corolla with ciliate tufts on the claws. The corolla is attached to the androecial base.
Figs. 4.77 - 4.79. *Modiola caroliniana*, pollen and fruit. Bars = 10 μm in 4.77, = 2 mm in 4.78 and 4.79.

4.77. The pollen is spheroidal and spiny.

4.78. Immature fruit.

4.79. Mature fruit. Each mericarp has two outwardly pointed spines and numerous trichomes. The sepals and bractlets persist.
gynoecium slightly exceeds the androecium in height. The stigmas are capitate (Fig. 4.75).

The pollen grains are spheroidal and spiny (Fig. 4.77). The flower symmetry is actinomorphic. The young fruit is covered with numerous long apically-pointed trichomes (Fig. 4.78). The mature schizocarp is segmented, covered with numerous trichomes, and has two outwardly directed spines or awns at the upper periphery of each mericarp. Each mericarp has an endoglossum, an internal appendage of the dorsal wall of the carpel which more or less completely divides the cavity. In the fruit, the sepals radiate upward and the bractlets radiate more or less outward (Fig. 4.79).

*Callirhoe involucrata* var. *Involucrata* -- Organography -- The plants are decumbent perennial herbs. The inflorescence is a raceme with flowers solitary in leaf axils. The pedicels are not jointed. The involucel consist of three green, distinct lanceolate to narrowly ovate bractlets. The five-lobed calyx is green and exceeds the bractlets in length. In the buds, the sepal apices are distinct, divergent, and form a tall projection. The five-merous corolla is deep red and spreads distally to form an open flower. Each petal has a white basal spot. The androecium is included and is antheriferous in the middle and upper portion of the column. The gynoecium is terminated by 14 - 23 introrsely decurrent stigmas. The fruits are indehiscent schizocarps with one seed per mericarp. The sepals and bractlets persist in the fruit (observations of collected material; Dorr, 1990). The flowers I examined were perfect, but Dorr (1990) noted that some may be male-sterile.

Initiation and early development of the involucel and calyx -- Floral buds initiate in the axil of a leaf and stipule pair (Figs. 4.80, 4.81). The floral
apex becomes convex, slightly elevated, and usually somewhat triangular in outline. The three bractlets initiate in a helical order on the periphery of the floral apex (Figs. 4.80, 4.81). No ring meristem is involved in bractlet initiation. Sometimes the bractlets appear at slightly different levels on the floral apex (Fig. 4.81). After all of the bractlets have initiated, the remaining pre-sepal apex develops a very low peripheral ring with a mounded center (Fig. 4.82). This stage looks similar to one of the stages precursory to formation of a ring meristem found in some other malvaceous taxa. The sepals are first apparent as a whorl of connate primordia that are separated from the remaining floral apex by a deep groove (Figs. 4.80, 4.83). The order of sepal initiation could not be ascertained. As the sepals enlarge they are basally fused and arch inward to partially cover the interior organs; but rather than merging apically into a single point, the lobes remain distinct and divergent (Figs. 4.88, 4.102). Each bractlet enlarges and develops a blade, but each remains distinct (Figs. 4.85, 4.88, 4.102).

Initiation and early development of the corolla and the androecium --

After all of the sepals have initiated, the pre-petal apex is initially convex (Fig. 4.83), but then a slight central depression develops (Fig. 4.84). For this taxon, it is not known if common mounded areas form or how the ring meristem arises. The earliest stage available already had a connate ring of ten common stamen primordia (Fig. 4.85). Associated pairs of these first common stamen primordia (a region) are positioned alternate to the sepals (Figs. 4.85, 4.86). As the petal-stamen ring meristem enlarges, subsequent partitioning in a centrifugal direction creates ten radial rows of common primordia (Figs. 4.87, 4.89 - 4.93). The five leading rows are more interior on the ring meristem than the five lagging rows (Figs. 4.89, 4.90). Petal initiation
is not apparent until after partitioning of the stamen portion of the ring meristem has resulted in approximately five common stamen primordia per radial row. The five petal primordia initiate very low on the outer flank of the petal-stamen ring meristem. One petal primordium initiates in each region of the ring meristem (Figs. 4.89, 4.90). This positions the petals alternate to the sepals and to the stamen groups. The order of petal initiation is simultaneous. Generally, six or seven common stamen primordia develop in each of the radial rows (Fig. 4.93). All of the common stamen primordia broaden laterally (many initiate as broad mounds), then each becomes two-lobed, then peanut-shaped, and then bifurcates in a lateral direction (Figs. 4.89 - 4.94). This process of bifurcation begins with the first-formed common stamen primordia and progresses basipetally down the elongating column until all of the common stamen primordia have divided. Prior to bifurcation, elongation of the tissue below most common primordia results in pairing of stamen primordia that share a common stalk basally (Fig. 4.96). As the androecial tube continues to elongate, the anthers and filaments form-differentiate (Figs. 4.94 - 4.96). At first there does not appear to be any space left on the interior surface of the petal-stamen ring meristem (Figs. 4.89, 4.90). However, in some flowers as anther differentiation occurs, sterile teeth appear at the apex of the androecial column (Figs 4.93, 4.94). The petal primordia become broad laterally, but elongation is delayed until after the anthers have externally discernible sporangia lobes (Fig. 4.95). The petals are adnate to the base of the androecial column (Fig. 4.95).

Initiation and early development of the gynoecium -- Initiation of the carpels begins after all of the common stamen primordia have initiated and the petal-stamen ring meristem has started to elongate vertically.
The gynoecium first appears as a whorl of 14 to 23 connate carpel primordia (Fig. 4.96). It is not known if a carpel ring meristem precedes initiation of the primordia. Carpel initiation is simultaneous. A large apical residuum persists to the interior of the gynoecial whorl (Fig. 4.96). With enlargement of the gynoecium, the apical residuum become concave (Figs. 4.97, 4.98). As the apical portion of the carpels begins to elongate, the androecium has elongated into a long column with filaments and anthers (Fig. 4.99). All of the carpels develop adaxial indentations (Fig. 4.96), then invaginations (Fig. 4.97), then crevices (Fig. 4.98), and then locules. One ovule develops in each locule. The syncarpous ovary develops lobes (Fig. 4.100), and then segmentation (Fig. 4.101) in accordance with the number of locules. The apical portion of the ovary develops long, centripetally directed trichomes. (Fig. 4.101). As the styles form, they are fused basally into a column and separate apically (Figs. 4.100, 4.101). A decurrent stigmatic surface develops on the inwardly-facing side of each style (Fig. 4.101).

Late stage and mature reproductive characters -- The involucellar bracts remain distinct and typically subtend the calyx (Fig. 4.102). In some flowers, one or more of the bracts may appear slightly lower than the others, but not conspicuously so. The calyx has glandular trichomes on the inner surfaces of the sepal bases (Fig. 4.101). At maturity, the sepals are fused 1/3 to 1/2 their length and extend beyond the involucellar bracts. The petals are distinct but are fused basally to the base of the androecial column (Fig. 4.103). Each petal base develops a pair of ciliate tufts. The corolla exceeds the calyx by 1/3 or less and flares distally to form an open flower.

In the androecium, the filaments diverge in basally fused pairs (Fig. 4.99). The pairs often appear to be in groups (Fig. 4.103). At maturity,
Figs. 4.80 - 4.85. *Callirhoe involucrata* var. *involucrata*, initiation of bractlets, sepals, and the androecium. Bars = 200 µm. 4.80. The bud to the right has initiated the first bractlet primordium (labeled 1). An arrow indicates where the apex has broadened for the second bractlet primordium. The bud to the left has five sepal primordia. A deep groove separates the sepal whorl from the remaining floral apex. 4.81. The bud to the right has three helically initiated bractlet primordia (sequence of initiation shown with numbers). The bractlet primordia are not all at the same level on the floral apex. The pre-sepal apex is convex. The large bud to the left has bractlet and sepal primordia. Each floral bud initiates in the axil of a leaf with a stipule pair. 4.82. The bud to the lower left has three sepal primordia inserted at different levels on the floral apex. A low sepal ring meristem is barely defined. 4.83. Five sepal primordia have initiated. The pre-petal apex is nearly pentagonal in outline and relatively flat. 4.84. Pre-petal floral apex with slight central depression. 4.85. The bractlets have elongated to become laminar. The petal-stamen ring meristem has ten common stamen primordia; an associated pair (region) is positioned alternate to the sepals (One associated pair is labeled with 1s).
Figs. 4.86 - 4.91. *Callirhoe involucrata* var. *involucrata*, development of bractlets and sepals, proliferation of stamens, and initiation of the petals. Bars = 200 μm. 4.86. The petal-stamen ring meristem is well-defined. The first ten common stamen primordia (1, only two labeled) have become radially broad. 4.87. Further partitioning of the androecial ring meristem has produced more common stamen primordia in a centrifugal direction (sequence of initiation shown with numbers). 4.88. The sepals have elongated and arch over the interior floral organs. The bractlets are inserted at slightly different levels below the calyx. 4.89. Centrifugal proliferation of common stamen primordia. Five of the radial rows of common stamens, the leading rows, are slightly more interior on the ring meristem than the alternating five lagging rows. Five petal primordia are present very low on the outer flank of the petal-stamen ring meristem. The petals initiate simultaneously, are alternisepalous, and on the same radii as the stamen groups. 4.90. Each region of the ring meristem bears five pairs of common stamen primordia and a petal (sequence of initiation of common stamen primordia shown with numbers in one region). Each of the older common stamen primordia is broad laterally. Occasionally, extra primordia are initiated (*). 4.91. Further expansion of the ring meristem with six pairs of common stamen primordia in each region (sequence of initiation shown with numbers in one region). The older common stamen primordia are two-lobed.
Figs. 4.92 - 4.97. *Callirhoe involucrata* var. *involucrata*, bifurcation of common stamen primordia, differentiation of anthers, and initiation of carpels. Bars = 200 \( \mu m \), except in 4.97 = 100 \( \mu m \). 4.92. The androecium has elongated into a short tube. The older common stamen primordia have bifurcated in a lateral direction. The younger common stamen primordia are peanut-shaped, two-lobed, or laterally broad. Petal elongation has been delayed. 4.93. Androecial tube with lateral bifurcation of most of the common stamen primordia. Small spaces remain on the upper portion of the androecial ring meristem. Some of the leading stamen rows have initiated an extra common stamen primordium. 4.94. Polar view of young androecial column. Small lobes (sterile teeth) have developed from the extra tissue on the ring meristem, now at the apex of the androecial column. Some differentiation of the anthers is apparent. 4.95. Stamen rows have become less distinct with further development of the anthers. Petals have broadened, but little elongation has occurred. 4.96. Gynoecium and partially dissected androecium. The tissue below each of the older common stamen primordia has elongated to form stalked common primordia. The gynoecium consists of a connate whorl of carpel primordia, each with a small adaxial indentation. The individual carpels are not very distinct on the raised carpel whorl which gives the appearance of a ring meristem. The apical residuum is relatively flat. 4.97. A connate whorl of carpel primordia. Each carpel primordium has a deep adaxial indentation. The apical residuum is concave.
Figs. 4.98 - 4.101. *Callirhoe involucrata* var. *involucrata*, development of the gynoeecium. Bars = 200 μm in 4.98 and 4.100, = 500 μm in 4.99 and 4.101. 4.98. Gynoeecium with 14 carpel primordia. Each primordium has a narrow adaxial invagination. 4.99. Gynoeecium and partial androecium. The stamens diverge from the column in basally fused pairs. The apex of the androecial column is antheriferous; no sterile teeth are present. The apical portion of each carpel has elongated slightly. Little petal elongation has occurred. Petals are adnate to the base of the androecium. 4.100. Young ovary that has the same number of lobes as locules. The styles are fused basally and divergent apically. 4.101. Immature gynoeecium. The ovary is segmented and the apical surface has numerous long trichomes. The styles are connate basally and free apically. Each style bears an introrsely decurrent stigma. The inner surface of each sepal base has numerous glandular trichomes.
Figs. 4.102 - 4.104. *Callirhoe involucrata* var. *involucrata*, mid and late stage floral characteristics. Bars = 2 mm. 4.102. Bud prior to anthesis. The bractlets are not fused. The sepals are fused basally and distinct and divergent apically, forming a projection above the major portion of the bud. 4.103. Mature flower with involucel and perianth removed. The anthers have dehisced by longitudinal slits at the sporangial sutures. Stamens occupy most of the column surface. Stamens diverge in partially fused pairs; often the pairs are clumped together into groups. Small tufts of trichomes are found at the lateral margins of each petal base. 4.104. Schizocarp with clearly defined mericarps. Part of the stylar column remains in the center of the fruit. Each mericarp has an apical incurved blunt beak.
stamens diverge from the upper 3/4 of the column. The apex of the column is antheriferous; there are no sterile teeth. The androecium is half the length of the corolla or less. The anthers dehisce by longitudinal slits between the sporangia (Fig. 4.103). The androecium typically has 120 to 140 stamens.

Each segment of the ovary develops a short blunt apical lobe that is directed centripetally. The long styles with introrsely decurrent stigmas extend conspicuously beyond the androecium. Pollen grains are spheroidal with numerous spines. The mature fruit is wider than tall with easily discernible mericarps. Each mericarp has an apical beak that is incurved (Fig. 4.104) and an inconspicuous endoglossum (internal process between the seeds). Both sepals and bractlets persist in the fruit, and the sepals radiate outward rather than clasp the fruit.

*Iliamna remota* — **Organography** — The plants are perennial herbs with much-branched erect stems. The flowers occur in small axillary clusters with nonjointed pedicels. The involucel consists of three green, linear bractlets. The five lobed-calyx is green and exceeds the involucel in length. The five-merous corolla is lavender to rose-colored and spreads distally to form an open flower. The androecium is included and is antheriferous at the top. The gynoecium is terminated by 11 to 15 capitate stigmas. The fruits are dehiscent schizocarps with two to four seeds per mericarp. The sepals and bractlets persist in the fruit (observations of collected material; Wiggins, 1936; Mohlenbrock, 1982).

*Initiation and early development of the involucel and calyx* — Usually several floral buds initiate sequentially in the axil of a leaf with stipule pair. The bractlet primordia initiate in helical sequence on the periphery of the floral apex (Fig. 4.105). The bractlet primordia initiate independently; no ring
meristem is involved. After all of the bractlet primordia have initiated, the sepal primordia initiate helically (Fig. 4.106). It is unknown if a ring meristem precedes sepal initiation. The sepals quickly equalize in size (Fig. 4.107), and elongate inward and upward to temporarily cover the interior floral organs (Fig. 4.108).

Initiation and early development of the corolla and the androecium -- With the development of the sepals, the pre-petal apex becomes convex and pentagonal in outline. Five common petal-stamen mounded areas develop alternate to the sepals (Figs. 4.107, 4.108). As these five common mounds become more defined, a low petal-stamen ring meristem develops. This is evident by the raised rim on the periphery of the apex which bears the five common mounds and a depression in the center of the apex (Figs. 4.109, 4.110). As the floral apex enlarges, the ring meristem and the five mounded areas become more pronounced (Fig. 4.111). At this time, five petal primordia initiate very low on the periphery of the petal-stamen ring meristem, one petal primordium at the outer base of each of the common mounded areas (Fig. 4.111). Petals initiate simultaneously. Usually, the surface of each of the common mounds develops a poorly defined radial groove (Fig. 4.112). At this time, ten common stamen primordia initiate on the interior surface of the ring meristem, with a pair on each of the five mounded areas or regions (Fig. 4.112). More common stamen primordia initiate in a centrifugal direction, thus usually forming ten radial rows of common stamen primordia, two rows in line with each petal (Figs. 4.113 - 4.118). Generally, five of the radial rows, the leading rows, begin slightly more interior on the ring meristem than the five alternating lagging rows. Six (Fig. 4.118) or even seven common stamen primordia may form in each of the radial rows. It is
common in the first and second sets of common stamen primordia to have large, laterally broad common primordia rather than lateral pairs (Figs. 4.113, 4.115, 4.116). In some flowers, the first set of common primordia may consist of irregular pairs with one long L-shaped primordium and one small round primordium (Figs. 4.115, 4.116, 4.122). With partitioning of the androecial ring meristem into common stamen primordia, no space appears to remain on the inner surface of the ring meristem (Fig. 4.114). As the ring meristem elongates into a short tube, each of the common stamen primordia becomes elliptical, then two-lobed, then peanut-shaped, and then bifurcates into two stamen primordia (Figs. 4.115 - 4.119). The direction of bifurcation is lateral except in the first set of common stamen primordia; in these most interior primordia the direction of bifurcation appears radial. The large common multistamen primordia (which may result in place of a lateral pair of common stamen primordia in the second set) become four-lobed (Fig. 4.116) and then quadrifurcate into four stamen primordia (Fig. 4.118). It is unclear what happens to the irregular pairs of common stamen primordia that may occur innermost on the ring meristem (Fig. 4.116). Division of the common primordia proceeds from the top of the androecial tube basipetally. As the androecium continues to elongate into a column, the anthers (Figs. 4.119 - 4.121) and the filaments (Fig. 4.125) differentiate. The young stamens diverge from the column in pairs and occupy the apex of the androecial column; there are no sterile teeth (Fig. 4.125). Petal primordia become broad laterally (Fig. 4.117), but do not become laminar until the anthers have differentiated (Figs. 4.121, 4.125). Elongation of the petals is delayed until sometime after the filaments begin to elongate.
Initiation and early development of the gynoecium — Initially, the precarpel apex is flat (Fig. 4.114). Then, as some of the common stamen primordia become lobed, the rim of the remaining floral apex becomes convex forming a low carpel ring meristem (Fig. 4.122). Without any significant enlargement of the ring meristem, the surface of the ring becomes uneven as the 11 to 15 carpel primordia initiate (Fig. 4.123). The carpel primordia initiate simultaneously in a single spatial whorl. A large apical residuum remains to the interior of the gynoecial whorl (Figs. 4.124, 4.126, 4.127). All of the carpels primordia develop adaxial indentations, then invaginations (Fig. 4.124), then crevices (Fig. 4.125), and then fertile locules (Figs. 4.126, 4.127). Two to four ovules develop in each locule (Fig. 4.127). After the ovules have initiated, the apical portions of the carpels elongate inwardly and upwardly to form styles that are free distally but fused basally (Fig. 4.127). The styles are of various heights, with no set pattern to the variation in height (Figs. 4.127, 4.128).

Late stage and mature reproductive characters — The involucellar bracts remain distinct and immediately subtend the calyx. The mature sepals are fused basally about 1/3 their length. The calyx exceeds the involucel in length. Glandular trichomes are found on the inner surface of the sepal bases. Petals are adnate to the base of the androecium (Fig. 4.129) and are generally double or a little less than double the length of the calyx. Each petal base has a pair of ciliate tufts. Petals form a contorted corolla in the bud, but at maturity they spread distally to form an open flower.

In the androecium, the filaments are densely arranged on the upper half of the androecial column. Filaments diverge singly, in pairs (often partially fused at the base), or in groups. Typically, the androecium has
Figs. 4.105 - 4.110. *Iliamna remota*, initiation of bractlets, sepals, common mounds, and petal-stamen ring meristem. Bars = 100 μm. 4.105. Floral apex with three helically initiated bractlet primordia (sequence of initiation shown with numbers). There is no bractlet ring meristem. 4.106. Three bractlet and five sepal primordia have initiated. Sepal initiation is helical (sequence of initiation is shown with numbers). The pre-petal apex is convex. 4.107. Sepals have nearly equalized in size. The pre-petal apex has barely defined mounds in positions alternate to the sepals. The center of the floral apex is convex. 4.108. The sepals have elongated and arch over the interior floral organs. 4.109. The center of the pre-petal apex is relatively flat. Five mounded areas are present along the periphery. 4.110. The pre-petal floral apex has a central depression and a peripheral raised ring meristem with five mounded areas.
Figs. 4.11 - 4.16. *Iliamna remot*a, proliferation of stamens and initiation of petals. Bars = 200 μm. 4.111. Common petal-stamen ring meristem with five broad mounds. Five petal primordia have initiated on the outer flank of the ring meristem; one petal primordium is at the base of each common mound or sectorial region. The order of petal initiation is simultaneous. 4.112. Some of the five common mounds have a shallow radial groove. 4.113. Partitioning of the ring meristem in a centrifugal direction. The overall pattern is ten radial rows of common stamen primordia, two rows on each of the original five common mounds or regions. In this flower bud and many others, deviations from this pattern have occurred. The deviations occur primarily in the first and second sets of common stamen primordia, where, rather than a lateral pair of common stamen primordia in a sectorial region, there is a single laterally broad common primordium. Petal primordia are present. 4.114. Partially dissected petal-stamen ring meristem. Each of the regions of the meristem have centrifugally initiated radial rows of common stamen primordia. There are leading and lagging rows. No spaces remain on the inner portion of the petal-stamen ring meristem. The gynoecium has not initiated. 4.115. The ring meristem has vertically elongated into a short tube. Up to five common stamen primordia are in each radial row. Many large common multistamen primordia are present in the first and second sets. 4.116. The oldest common primordia are lobed in accordance with the number of stamens they will produce.
Figs. 4.117 - 4.123. *Iliamna remota*, proliferation of stamens, differentiation of anthers and petals, and initiation of the gynoecium. Bars = 250 µm, except in 4.122 = 100 µm. 4.117. Lateral view of a short androecial tube. Most of the older common stamen primordia have divided (bifurcated or quadrifurcated). Petal primordia have broadened laterally. 4.118. Polar view of a short androecial tube. The older common stamen primordia have furcated. The direction of this division may be radial or lateral for the first set of common stamen primordia, but for the later-formed common stamen primordia, the direction of division is lateral. The youngest common stamen primordia are peanut-shaped, two-lobed, or elliptic in shape. Each radial row of staminal primordia has six members. 4.119. Slightly older androecial column with the last-formed common stamen primordia at various stages of bifurcation. The first-formed stamen primordia are apically broad as they start anther differentiation. Petals still appear as laterally broad primordia. 4.120. Further differentiation of anthers. 4.121. Androecial column with differentiated anthers. The petals are laminar but little elongation has occurred. 4.122. Initiation of a carpel ring meristem interior to the androecium. The periphery of the partial apex is slightly raised (at arrows). Individual carpel mounds are not apparent. 4.123. Interior to the androecium, the rim of the floral apex is mounded (at arrow) and the center of the apex is flat. Initiation of carpel primordia is indicated by the slightly uneven surface of the gynoecial ring meristem. The short androecial tube has common stamen primordia. No spaces remain on the upper interior surface of the petal-stamen ring meristem.
Figs. 4.124 - 4.127. Iliamna remota, development of the gynoecium. Bars = 250 μm. 4.124. Twelve connate carpel primordia (C, only two labeled). Each carpel primordium has an adaxial indentation. A large apical residuum remains in the center of the gynoecial whorl. 4.125. Partially dissected androecial column with some of the filaments diverging in pairs. Each carpel primordium has a deep crevice. Petals are laminar but elongation has been retarded. 4.126. Gynoecium with locular crevices. An ovule is visible at the arrow. The apical residuum is present. 4.127. Gynoecium with short, hollow stylar column. The styles are fused basally but free distally. Each locule contains several ovules. The apical residuum is still present.
Figs. 4.128 - 4.131. *Iliamna remota*, late stage floral characteristics, pollen, and partially dissected young fruit. Bars = 1 mm, except 4.130 = 50 μm. 4.128. Immature gynoecial column and partially dissected androecium. The ovary has the same number of lobes as locules, and numerous immature trichomes. The styles are basally fused and apically divergent. The styles are of various heights; there is no particular pattern to their height. Filaments diverge in basally fused pairs. 4.129. The suture between the sporangia of each anther has begun to dehisce and release pollen. The androecial and gynoecial columns have not fully elongated. The apical portion of each style has broadened but the stigmatic surface has not developed. 4.130. Anther at time of dehiscence. Pollen grains are spheroidal to suboblate, spiny, and colporate. 4.131. Dissected young fruit. Each mericarp has two to four seeds and no endoglossum.
between 120 and 140 stamens and is about 2/3 as tall as the corolla. Despite how frequently common multistamen primordia occur during the early stages of androecial development, almost all of the stamens are bisporangiate (Figs. 4.121, 4.128, 4.129). Rarely, two stamens are conjoined with a double-wide filament and four anther sacs. No sterile teeth are present at the apex of the androecium (Figs. 4.128, 4.129). Anthers dehisce longitudinally at the sutures between the sporangia. The anthers begin to dehisce before the stigmas are mature and before the gynoecium has fully elongated (Fig. 4.26).

The ovary develops lobes and then segments in the same number as locules. The ovary surface develops short trichomes (Fig. 4.128) that become long upwardly pointing hairs at maturity. The basal portion of the styles fuse into a column above the ovary, but apically the styles diverge from the column at various levels and elongate to various heights (Figs. 4.128, 4.129). Typically, the styles are fused about half their length. The capitate stigmas are usually wedge-shaped. The pollen grains are spheroidal or suboblate, spiny, and colporate (Fig. 4.130). The schizocarps are wider than tall and are covered with stiff hairs. The sepals and bractlets cup upward around the fruit. Each mericarp has several seeds and lacks endoglossa (Fig. 4.131).

**Lavatera trimestris** — **Organography** — The plants are shrubs or small trees with solitary flowers in leaf axils. The pedicels are not jointed. The involucel consist of three green, connate, foliaceous bractlets. Each mature bractlet has several apical lobes. The calyx is green, five-lobed, and slightly longer than the involucel. The five-merous corolla is lavender and spreads distally to form an open flower. The androecium is included and
is antheriferous in the upper portion. The gynoecium is terminated by ten to 16 introrsely decurrent stigmas. The fruits are indehiscent schizocarps with one seed per mericarp. Sepals and bractlets persist in the fruit (observation of collected material; Correll and Johnston, 1979; Ray, 1995).

**Initiation and early development of the involucre and calyx** -- A floral apex initiates in the axil of a leaf with paired stipules. Prior to organ initiation, the floral apex is circular, convex, and slightly elevated (Fig. 4.132). The upper portion of the floral bud broadens and the lower portion forms a short stalk. At this time, a bractlet ring meristem forms around the periphery of the apex. The ring meristem appears as a sloping ledge separated from the rest of the mounded apex by a shallow depression (Fig. 4.133). Three sepal primordia initiate helically on the ring of meristematic tissue (Figs. 4.133, 4.134). In early development, the bractlets form a low cup with three projections that point upward and slightly inward over the other developing organs (Figs. 4.134 - 4.137). The pre-sepal apex is initially convex and circular in outline (Fig. 4.134). Then a sepal ring meristem develops around the periphery of the apex. This sepal ring meristem is a mounded rim separated from the rest of the convex apex by a depression (Fig. 4.135). On this sepal ring meristem, five sepal primordia initiate (Figs. 4. 132, 4.136). The order of sepal initiation could not be ascertained. As the sepals enlarge, they are fused basally and arch distally inward to cover the interior floral apex temporarily.

**Initiation and early development of the corolla and the androecium** -- The pre-petal apex is initially convex and circular in outline (Fig. 4.135), then as sepals develop it becomes pentagonal in outline (Fig. 4.136) and develops a central depression (Fig. 4.137). The periphery of the apex
enlarges into a large petal-stamen ring meristem (Fig. 4.138). In this taxon, although the corners of the pentagonal apex may become slightly elevated in the early stages of ring meristem formation, they do not form delineated mounds. As the ring meristem enlarges, the upper surface is partitioned by ten radial grooves (Fig. 4.139). Subsequent partitioning in a centrifugal direction creates ten radial rows of common stamen primordia, five leading and five lagging rows (Figs. 4.140 - 4.141). Rather than the pairs of common stamen primordia in each group being positioned beside each other, they are somewhat oblique (Figs. 4.140 - 4.141). There are no spaces remaining on the interior surface of the ring meristem (Figs. 4.140, 4.141, 4.146). Petal initiation occurs during centrifugal partitioning of the androecial portion of the ring meristem. The five petal primordia initiate in a simultaneous order on the outer flank of the ring meristem (Fig. 4.140). Petals are in line with the stamen groups and positioned alternate to the sepals. Typically, five common stamen primordia initiate in each radial row (Figs. 4.141, 4.142). As the ring meristem elongates into a short tube, each of the common stamen primordia becomes elliptically broad, then two-lobed, then peanut-shaped, and then bifurcate into two stamen primordia (Figs. 4.141 - 4.143). The direction of this bifurcation is lateral except in the first set of common primordia where the direction is radial to obliquely radial (Figs. 4.142, 4.146). This process of bifurcation begins with the first-formed common primordia and progresses centrifugally until all of the common stamen primordia are divided. As differentiation of the anthers occurs, small areas of sterile tissue are present at the apex of the androecial column (Figs. 4.143, 4.144). It is not until the sporangia become easily discernible externally on the anthers that petal primordia become laminar; (Fig. 4.145) petal elongation is
retarded until even later. Petals are basally adnate to the base of the androecial column (Fig. 4.145).

**Initiation and early development of the gynoecium** -- The pre-carpel apex is flat (Fig. 4.146). As the anthers begin to differentiate, the gynoecium initiates as a raised continuous ring of tissue (Fig. 4.147). With further development, the ten to 16 carpel primordia become distinguishable by small indentations on the inner side of the ring meristem (Fig. 4.148). Carpel initiation is simultaneous. A large apical residuum persists interior to the gynoecial whorl (Figs. 4.148 - 4.150). All of the carpel primordia develop adaxial invaginations (Fig. 4.149) and then locules (Fig. 4.150). One ovule initiates in each locule. As the apical portions of the carpel elongate into a basally fused stylar column, the ovary develops lobes (Fig. 4.151) and then segments (Fig. 4.152) in number equal to locule number. Differentiation of the stigmas does not occur until after the sutures between sporangia of the anthers begins to dehisce (Fig. 4.152).

**Late stage and mature reproductive characters** -- At maturity, the bractlets fused basally 1/2 to 3/4 their length. Each bractlet usually has several apical lobes. In the buds, the sepals form a protective dome over the interior organs. At maturity, the sepals are fused basally about 1/3 their length and exceed the involucel slightly. The inner surfaces of the sepal bases have glandular trichomes. Petals remain distinct from each other but adnate to the base of the androecium. Each petal base has a pair of ciliate tufts. The corolla height is two to three times that of the calyx and spreads distally to form an open flower.

The longitudinal sutures between sporangia in the anthers begin to dehisce even before the androecial column has reached full height.
Figs. 4.132 - 4.137. *Lavatera trimestris*, initiation of bractlets, sepals, and petal-stamen ring meristem. Bars = 100 μm. **4.132.** Two floral apices (A), each in the axil of a leaf and paired stipules. The shoot apex (SA) is in the center of the micrograph. The floral apices are vertically elevated, round in outline, and convex. **4.133.** The floral apex has an elevated base or stalk (at arrow) and a bractlet ring meristem around the periphery. The ring meristem appears as a peripheral ledge separated from the convex apex by a slight depression. A bractlet primordium has initiated on the bractlet ring meristem. **4.134.** Three helically initiated bractlet primordia (sequence of initiation shown with numbers). The pre-sepal apex is convex. **4.135.** Sepal ring meristem. Some sepal primordia are present. Bractlet primordia are fused basally into a low cup. **4.136.** Five sepal primordia. The pre-petal apex is convex and pentagonal in outline. **4.137.** Pre-petal apex with a central depression (at arrow). This is an early stage of formation of the petal-stamen ring meristem.
Figs. 4.138 - 4.143. *Lavatera trimestris*, initiation of petals and proliferation of stamens. Bars = 100 μm. 4.138. Petal-stamen ring meristem. 4.139. The petal-stamen ring meristem is apically partitioned by ten radial grooves. 4.140. Ten radial rows of centrifugally initiated common stamen primordia (sequence of initiation shown with numbers in one sectorial region). The leading rows start more interior on the ring meristem and have each initiated one more common primordium than the lagging rows. Five petal primordia are present on the outer flank of the common petal-ring meristem. The common stamen groups are in line with the petals. Rather than the pairs of common stamen primordia in each group positioned laterally, they are slightly oblique. No spaces remain on the interior surface of the ring meristem. 4.141. Five common stamen primordia are present in each radial row. The first set of common stamen primordia are broad radially, all other sets of common stamen primordia are laterally broad. 4.142. The common stamen primordia are in various stages of bifurcation; the earlier formed sets have progressed further. 4.143. Bifurcation of common stamen primordia is nearly complete. The oldest individual stamen primordia are broad apically. Petal primordia are broad laterally, but elongation has been retarded. Some space remains at the top of the androecial tube.
Figs. 4.144 - 4.149. *Lavatera trimestris*, development of the androecium and corolla and initiation of the gynoecium. Bars = 250 μm in 4.144 and 4.145, = 100 μm in 4.146 - 4.149. 4.144. Differentiation of the anthers. The surface of each anther has two barely defined sporangia. A small amount of sterile tissue is present at the apex of the androecial column. 4.145. The two sporangia per anther are easily discernible. Petals are laminar, but elongation has been retarded. 4.146. The pre-carpel apex is flat. There is no space remaining on the interior surface of the androecium. 4.147. Initiation of the gynoecium as a raised continuous ring of tissue. The inner surface of the ring meristem is uneven. An apical residuum remains. 4.148. A whorl of 13 carpel primordia. Each carpel primordium has an adaxial indentation. 4.149. Fifteen carpel primordia in a connate whorl. Each carpel primordium has an adaxial invagination. The apical residuum is slightly convex.
Figs. 4.150 - 4.153. *Lavatera trimestris*, development of the gynoecium and late stage floral characteristics. Bars = 1 mm, except in 4.150 = 500 μm. 4.150. Gynoecium with locular cavities and partially dissected androecial column. Barely defined sterile teeth are present at the apex of the androecial column. 4.151. Young gynoecial column with a lobed ovary and a short, basally-fused stylar column. Petals have elongated somewhat. 4.152. Gynoecium with segmented ovary and long basally fused stylar column. The sutures between the sporangia of the anthers have started to dehisce. Many filaments diverge in pairs. 4.153. Introrsely decurrent stigmas and dehisced anthers.
Figs. 4.154 - 4.155. *Lavatera trimestris*, pollen and fruit. Bars = 50 μm in 4.154, = 2 mm in 4.155. 4.154. Pollen grains are spheroidal, spiny, and polyporate. 4.155. Schizocarp. The tissue from the lower portion of the stylar column and the upper portion of the ovary have inflated to form a cap over the mericarps. Both bractlets and sepals persist and often they enclose the fruit (some sepals and bractlets have been removed).
Filaments diverge from the column in pairs (often basally fused) or sometimes singly or in groups (Figs. 4.151, 4.152). At maturity, the filaments radiate from the upper half of the column and there are no sterile teeth. The androecium typically has close to 100 stamens and is between 1/3 and 1/2 as tall as the corolla.

As the gynoecium reaches maturity, the upper portion of the ovary and the lower portion of the stylar column enlarge to extend radially to form a cap over the locular segments of the ovary. Long thin introrsely decurrent stigmas extend beyond the androecium (Fig. 4.153). The pollen grains are spheroidal, polyporate, and echinate (Fig. 4.154). Flower symmetry is actinomorphic. The mature schizocarp is wider than tall. The cup-shaped calyx and involucel persist in the fruit and may partially enclose the fruit (Fig. 4.155). In the fruit, the ovary cap becomes marginally inflated with a depressed central region bearing a small stylar column stump; this cap is positioned over the mericarps (Fig. 4.155).

**Anisodontea X hypomandarum -- Organography --** The plants are branched shrubs with one to three flowers in leaf axils. The involucel consist of three green, distinct, linear bractlets. The five-lobed calyx is green and slightly exceeds the involucel in length. The five-merous corolla is mauve-pink with magenta at the base. The corolla spreads to form a relatively flat whorl. The androecium is included and is antheriferous at the top. The gynoecium is terminated by 10 to 12 capitate stigmas. The fruit is a schizocarp with one seed per mericarp and persistent sepals and bractlets (observations of collected material; Bates, 1969). Contrary to the general characteristics for this hybrid outlined by Bates (1969), this
collection did not have jointed pedicels, occasional two-seeded locules, or endoglossa in the mericarps.

**Initiation and early development of the involucel and calyx** -- Floral buds initiate in the axil of a leaf with stipule pair (Fig. 4.156). As the tissue beneath each floral apex elongates to form a stalk, bractlet primordia initiate on the periphery of the floral apex (Fig. 4.156). The three bractlet primordia initiate helically without a ring meristem (Fig. 4.156). After all of the bractlets have initiated, the five sepal primordia initiate in helical sequence (Figs. 4.157, 4.158). No sepal ring meristem is present (Fig. 4.157). As the sepals enlarge, they are connate basally (Fig. 4.167) and arch inward apically to temporarily cover the interior organs (Fig. 4.162). In early development, the bractlets are distinct, immediately subtend the calyx (Figs. 4.158, 4.160, 4.162), and elongate upward (Fig. 4.162).

**Initiation and early development of the corolla and androecium** -- The apex to the interior of the sepals is initially convex (Fig. 4.159), but as the sepals elongate it develops a central depression (Fig. 4.160). The periphery of the apex enlarges into a large petal-stamen ring meristem (Fig. 4.161). Well delineated common mounds are lacking prior to and during formation of this ring meristem. As the ring meristem enlarges, the apical portion becomes partitioned by ten radial grooves (Fig. 4.163). At this time, the five petal primordia initiate at the outer flank of the ring meristem (Fig. 4.163). Petal initiation is simultaneous. Subsequent partitioning of the androecial portion of the ring meristem in a centrifugal direction creates ten radial rows of common stamen primordia, five leading and five lagging rows (Fig. 4.164). The petals are in line with the paired stamen rows. There are no spaces remaining on the interior surface of the ring meristem (Fig. 4.164).
Typically, four common stamen primordia form in each of the radial rows (Fig. 4.166). As the ring meristem elongates into a short tube, each of the common stamen primordia bifurcates to yield two stamens (Figs. 4.165 - 4.167). The direction of this bifurcation is obliquely lateral except in the first set where the direction may be obliquely radial to radial (Fig. 4.166). While the androecium is a short tube, the apical remains of the ring meristem has small areas of sterile tissue (Fig. 4.166) which may later form minute sterile teeth (Figs. 4.168 - 4.170). Elongation below the peanut-shaped common stamen primordia during bifurcation often results in stamen pairs that have basally fused filaments (Figs. 4.166 - 4.169). Petal elongation is retarded until after the anthers and filaments have started to differentiate and the filaments have begun to elongate (Figs. 4.167, 4.170).

Initiation and early development of the gynoecium -- The gynoecium initiates during the early stages of anther differentiation. It is first evident as a connate whorl of carpel primordia, each with an adaxial indentation (Fig. 4.168). It is unknown if a ring meristem precedes carpel initiation. Carpel initiation is simultaneous. An apical residuum remains to the interior of the gynoecial whorl (Figs. 4.1.65 - 4.169). Each carpel primordium develops adaxial crevices (Fig. 4.169) and then uniovulate locules (Fig. 4.170). Differentiation of the styles and stigmas begins prior to exsertion beyond the anthers (Fig. 4.172).

Late stage and mature reproductive characters -- In the mid and late stages of floral development, elongation of the receptacle between the involucel and the calyx causes vertical separation between the two whorls (Fig. 4.171). At maturity, the involucel may be positioned 1-2 mm below the calyx. The bractlets remain distinct and radiate upward and outward.
The calyx forms a protective dome in the bud (Figs. 4.170, 4.171). Glandular trichomes develop on the inner surfaces of the sepal bases (Fig. 4.170). At anthesis, the calyx exceeds the involucel in height slightly and the lower half is connate. As the petals elongate, they temporarily form a contorted corolla (Figs. 4.171, 4.172). At maturity, the corolla spreads to form a relatively flat whorl that is adnate to the androecial column at the level of the ovary crest (Fig. 4.174). The corolla is approximately double the length of the calyx and each petal base has a pair of ciliate tufts.

Most of the filaments diverge from the androecial column in basally fused pairs, although some may appear singly, in unfused pairs, or in groups (Figs. 4.172, 4.173). At maturity, the filaments radiate from the upper third of the androecial column (Fig. 4.174), a ring of trichomes circles the column just below divergence (Fig. 4.174), and the anthers dehisce by longitudinal slits at the sporangial sutures (Figs. 4.173, 4.174). Even though minute sterile teeth are present in earlier stages of development, at maturity sterile teeth are lacking at the apex of the androecial column (Fig. 4.173). The androecium typically has around 80 stamens and is about half the height of the corolla.

The mature gynoecium slightly exceeds the androecium in height (Fig. 4.174). The ovary surface is segmented, lacks long trichomes or appendages, and has two apical incurved lobes on each segment (Fig. 4.177). Long thin styles diverge from the upper quarter of the pistil (Fig. 4.174) and each bears a capitate stigma (Fig. 4.175). The pollen grains are spheroidal, echinate, and zonocolporate (Fig. 4.176). The schizocarp is wide than tall with persistent sepals and bractlets.

*Abutilon parishii* — **Organography** — The plants are subshrubs with solitary flowers in axils of leaves. The flowers have jointed pedicels and
Figs. 4.156 - 4.161. Anisodontea X hypomandarum, initiation of bractlets, sepals, and petal-stamen ring meristem. Bars = 100 μm. 4.156. Floral shoot with flowers initiating in the axils of leaves with stipules. The floral bud in the upper left corner has an elongated stalk (at arrow) and two bractlet primordia, one large and one small (sequence of initiation shown with numbers). The bud on the right has three bractlet primordia and one sepal primordium. No bractlet or sepal ring meristems are present. 4.157. Polar view of flower bud (from previous micrograph) with initiation of one sepal primordium. Three bractlet primordia are present. 4.158. Five helically initiated sepal primordia (possible sequence of initiation shown with numbers). 4.159. Five sepal primordia (only one labeled). The pre-petal apex is convex and pentagonal in outline. 4.160. Pre-petal apex with a central depression. The apex does not have any prominent common mounds. The bractlets are adjacent to the calyx whorl. 4.161. Common petal-stamen ring meristem. The surface of the ring meristem is smooth (aside from some damaged areas).
Figs. 4.162 - 4.165. *Anisodontea X hypomandarum*, development of bractlets and sepals; initiation of petals; and proliferation of the androecium. Bars = 200 μm. 4.162. Young flower bud with sepals temporarily forming a protective cover over the interior organs. Bractlets are distinct and immediately subtend the calyx. 4.163. The apical portion of the ring meristem has ten radial grooves. Five petal primordia have initiated on the outer flank of the ring meristem. 4.164. Ten radial rows of centrifugally initiated common stamen primordia (sequence of initiation is shown with numbers in one sectorial region). Petal primordia are in line with the paired common stamen primordia rows. No space remains on the upper interior surface of the ring meristem. 4.165. The common stamen primordia are elliptic and some are two-lobed. The petal primordia are alternate to the sepals.

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Figs. 4.166 - 4.171. *Anisodonteia X hypomandarum*, proliferation of the androecium, initiation of the gynoecium, and midstage floral characteristics. Bars = 100 μm in 4.166 - 4.169, = 500 μm in 4.170, = 2 mm in 4.171. 4.166. Four common stamen primordia have initiated in each radial row. The older common stamen primordia are peanut shaped, two-lobed, or elliptic. A small amount of sterile tissue (R) is visible at the apex of the androecial tube. 4.167. Most of the common stamen primordia have bifurcated. Each pair of stamen primordia share a common elevated base. Petal elongation has been retarded. The calyx is basally connate. 4.168. Gynoecium and partially dissected androecial tube. The gynoecium is a whorl of ten connate carpel primordia, each with an adaxial indentation. Small sterile teeth are present at the apex of the androecial tube. Most of the stamen primordia are in basally fused pairs. Each stamen primordium is apically broad with the start of anther differentiation. 4.169. Gynoecium with locular crevices. Filaments and anthers are partially differentiated. 4.170. Longitudinal section of young flower bud. Ovules have initiated in the syncarpous ovary. Petal elongation has been retarded. Glandular trichomes have initiated on the inner sepal bases (N). 4.171. Immature flower bud. The sepals have formed a protective dome. Petals are overlapped. The bractlets are inserted a short distance below the calyx whorl.
Figs. 4.172 - 4.177. *Anisodontea X hypomandarum*, midstage and mature floral characteristics. Bars = 1 mm in 4.172, 4.174, and 4.177, = 500 μm in 4.173, = 50 μm in 4.175 and 4.176. 4.172. Petals have surpassed the androecium and gynoecium. Petals are adnate to the androecium base. Stamen filaments have elongated, but the androecial column is still short and has a ring of trichomes below filament divergence. Capitate stigmas have differentiated. 4.173. Apex of androecial column at anthesis. No teeth are present. Most filaments diverge in basally fused pairs, although some may be single or in groups. Anthers have dehisced by longitudinal slits at the sporangial sutures. 4.174. Androecial and gynoecial columns at anthesis. The androecium has a ring of trichomes below the level of filament divergence. Petal scars show that the corolla is adnate to the androecium and that the petals are positioned at or above the ovary crest. The styles have stigmas and are exserted beyond the anthers. 4.175. Capitate stigma. 4.176. Pollen grains are spheroidal, echinate, and zonocolporate. 4.177. Segmented ovary. Each locular segment has two apical incurved lobes. The upper portion of the stylar column has been removed.
lack involucels. The calyx is five-lobed, green, and persists in the fruit. The five-merous corolla is pale yellow to yellow-orange and spreads to form an open flower. The androecium is included and is antheriferous only at the apex. The gynoecium is terminated by six to nine capitate stigmas. The fruits are dehiscent schizocarps with three seeds per mericarp (observation of collected material; Fryxell, 1993).

**Initiation and early development of the calyx** – A floral bud initiates in the axil of a leaf and stipule pair. As the receptacular tissue beneath each floral apex elongates into a short stalk, sepal initiation begins. Sepal primordia initiate helically on the periphery of the floral apex without a ring meristem (Figs. 4.178, 4.179). As the sepals enlarge, they arch inward to cover the interior floral organs temporarily (Fig. 4.178).

**Initiation and early development of the corolla and the androecium** – The pre-petal apex is initially convex and pentagonal in outline (Figs. 4.178, 4.179), then it becomes relatively flat with a central depression (Fig. 4.180). It then develops a petal-stamen ring meristem (Fig. 4.181). Well delineated common primordial mounds are lacking prior to or during early formation of the ring meristem. After formation of the petal-stamen ring meristem, the upper portion of the ring meristem becomes radially partitioned into five common mounds (Fig. 4.182). Concurrently, the five petal primordia initiate on the lower outer flank of the ring meristem (Fig. 4.182). Petal initiation is simultaneous. The five common mounds and the petals are alternate to the sepals. Next, each of the five common mounded areas develops a radial groove so that the upper portion of the ring meristem is divided into ten mounds (Fig. 4.183). Subsequent partitioning of the androecial portion of the ring meristem in a centrifugal direction creates ten radial rows of common
stamen primordia, five leading and five lagging rows (Figs. 4.184 - 4.186). Typically, three common stamen primordia form in each radial row (Fig. 4.186). At this stage, there are no spaces remaining on the interior upper surface of the ring meristem (Figs. 4.184 - 4.187, 4.190). Each common stamen primordium bifurcates to yield two stamen primordia (Figs. 4.188, 4.189). The direction of this bifurcation is radial (centripetal) for the first-formed common stamen primordia on the inner portion of the ring meristem and oblique for the other sets of common stamen primordia (Figs. 4.186, 4.187). During differentiation of the anthers, the petal primordia become laminar (Figs. 4.189, 4.192), but elongation is retarded until later in floral development. With stamen differentiation, two filaments are often fused basally (Fig. 4.192).

Initiation and early development of the gynoecium -- The gynoecium initiates during the early stages of common stamen bifurcation. It is first evident as a whorl of connate carpel primordia, each with an adaxial indentation (Fig. 4.190). It is unknown if a ring meristem precedes carpel initiation. Carpel initiation is simultaneous. Each carpel primordium develops a fertile locule with three ovules (Figs. 4.191 - 4.193). An apical residuum remains to the interior of the gynoecial whorl (Fig. 4.191). The apical portions of the carpels elongate into a basally fused stylar column (Figs. 4.192, 4.193).

Late stage and mature reproductive characteristics -- At anthesis, the lower 1/3 of the sepals are partially connate. Glandular trichomes develop on the inner surfaces of the sepal bases. As the petals elongate, they temporarily form a contort corolla, which is adnate to the base of the androecium. At maturity, the petals spread to form an open corolla that is
Figs. 4.178 - 4.183. *Abutilon parishii*, initiation of sepals, petal-stamen ring meristem, and petals. Bars = 100 μm. 4.178. Floral shoot showing three developmental stages of sepals. The lower floral apex has one sepal primordium. The upper left bud has five sepal primordia and a convex pre-petal apex. The upper right bud has five sepal primordia that have elongated and that arch inward over the interior organs. 4.179. Initiation of sepal primordia on the periphery of the floral apex (possible sequence of initiation shown with numbers). No sepal ring meristem is present. A short receptacular stalk has developed beneath the floral apex. 4.180. Pre-petal apex with slightly depressed center. 4.181. Common petal-stamen ring meristem. 4.182. The petal-stamen ring meristem has five radial grooves dividing the upper portion of the ring meristem into five common mounds. Five petal primordia are present at the outer flank of the ring meristem. Petals and common mounds (only one sectorial region labeled) are positioned alternate to the sepals. 4.183. The upper portion of the ring meristem is partitioned by ten radial grooves. Petal primordia have become more defined.
Figs. 4.184 - 4.189, *Abutilon parishii*, proliferation of stamens. Bars = 100 μm, except 4.189 = 500 μm. **4.184.** Initiation of the first ten common stamen primordia on the inner portion of the petal-stamen ring meristem (1, two labeled in one region of the ring meristem). **4.185.** Centrifugal initiation of common stamen primordia on the ring meristem (sequence of initiation shown with numbers in one region). The first set of common stamen primordia are radially broad. **4.186.** The first set of common stamen primordia are radially two-lobed. The second and third sets of common stamen primordia are laterally elliptic. **4.187.** Bifurcation of common stamen primordia. **4.188.** Anthers are in the early stages of differentiation. **4.189.** Petals are laminar, but elongation has been retarded. Anthers have differentiated.
Figs. 4.190 - 4.195. *Abutilon parishii*, gynoecial development and late stage floral characteristics. Bars = 100 μm in 4.190 and 4.191, = 500 μm in 4.192 - 4.194, = 50 μm in 4.195. 4.190. Gynoecium and partially dissected androecial ring meristem. Carpel primordia are present in a low connate whorl (C, only one labeled). No spaces are present on the inner surface of the androecial ring meristem. 4.191. Initiation of ovules in the locules. An apical residuum is present. 4.192. Syncarpous ovary with short apical stylar projections. Stamens diverge from the column in pairs with basally fused filaments. No teeth are present at the apex of the androecium. 4.193. Three ovules are developing in each locule. A basally fused stylar column has developed. 4.194. Androecial column prior to anthesis. Stigmas are capitate. 4.195. Pollen grains are spheroidal to suboblate, echinate, and zonocolporate.
approximately double the length of the calyx. Each petal base has a pair of ciliate tufts.

All of the filaments radiate from the apex of the androecial column and no sterile teeth are present. The filaments appear to diverge in five big groups, often with paired filaments that are basally fused. In some of the last-formed stamens, two filaments are sometimes conjoined to the point of anther attachment. The androecium typically has about 60 stamens and is about half as tall as the corolla. Anther dehiscence is by longitudinal slits at the sporangial sutures.

The mature gynoecium slightly exceeds the androecium in height. The ovary surface is segmented, covered with trichomes, and has one apical appendage per carpel segment. Each style has a capitate stigma (Fig. 4.194). Pollen grains are spheroidal to suboblate, echinate, and zonicolporate (Fig. 4.195). The height of the schizocarps approximately equals or slightly exceeds the width. Each mericarp has numerous trichomes and an apical spine that points up and outward (these spinal appendages are divided in two as the mericarp dehisces). The sepals persist and clasp the base of the fruit.

**DISCUSSION**

The involucel — Several characteristics of the involucels are variable among taxa in the Malveae. Two species of those studied, *Sida rhombifolia* and *Abutilon parishii*, lack involucels. The other taxa examined have a three-merous involucel. When present, the bractlets are green, shorter than the calyx, and in most taxa they are unfused and generally narrow. *Lavatera trimestris* is the exception with broad bractlets that are fused more than half their length.
Position of the involucre in regard to the calyx is variable. In most taxa the bractlets are positioned in a whorl immediately adjacent to the calyx. There are, however, several exceptions to this. In *Anisodonte X hypomandarum* all of the bractlets are usually positioned a short distance below the calyx on the swollen receptacle above the pedicel. *Callirhoe involucrata var. involucrata* may have one or more of the bractlets positioned slightly below the calyx on the receptacle. Four species of *Callirhoe* (Dorr, 1990), three species of *Anisodonte* (Bates, 1969), and *Malvella leprosa* (Fryxell, 1988) have one or more of the involucrel bractlets positioned below the calyx. In *Anisodonte triloba*, which has five bract structures, Bates (1969) describes three of the structures that are closest to the calyx as involucral (involucrel) bracts and two other structures which appear further down on the pedicel as probably sterile bracts of the cyme. At the other extreme, Dorr (1990) reported that *Callirhoe triangulata* has bractlets that are sometimes adnate to the calyx. Bates (1969) also reported that in *Anisodonte anomala*, the involucreal bracts (involucrel bracts) are adnate to or joined with, or even form a single monophyllous whorl with the calyx. Several species in the Gossypieae, *Thespesia populnea, Thespesia beatensis, Lebronnecia kokioides,* and *Hampea rovirosae,* have bractlets that initiate at slightly different levels on the floral apex (Ch. 3; Fryxell, 1979). In all of the taxa I examined, the bractlet primordia clearly initiate on the floral apex. The spacial separation from the calyx can be accounted for in part by the bractlet primordia initiating at slightly different levels on the floral apex and/or by subsequent elongation of the receptacle between the calyx and involucel. For the reasons I outlined in Chapters 2 and 3, the bractlets are more likely homologous to the sepals than to leaves; but rather than
being considered as extra sepals, they should be considered as discrete floral organs. Further investigation is needed to determine origin and homology of the bract or bractlet structures that have been reported by Bates (1969), Dorr (1990), and Fryxell (1979) as joined to the calyx or spaced much further down the pedicel.

In representatives of this tribe, initiation of the involucel begins after the flower stalk or pedicel has started to elongate. Bractlet initiation is helical, although the plastochron interval may vary between consecutive organ initiations. Most of the taxa have bractlets that initiate without a ring meristem; only *Lavatera trimestris* has a bractlet ring meristem. In my examination of representatives of the other tribes of Malvaceae (Chs. 2, 3), bractlet initiation was consistently helical. Presence of a bractlet ring meristem varied among taxa in the Malvavisseae and Hibisceae, but it was consistently absent in the Gossypieae.

Previous literature is contradictory about the order of bractlet initiation and the presence or absence of a bractlet ring meristem. Payer (1857) reported that the bractlets all arise as distinct primordia in an order similar to leaves and stipules. He reported that Duchartre (1845) thought there was a bractlet ring meristem that later became separated into primordia. Sattler (1973) described the involucel in *Alcea rosea* with six primordia that “appear in an extremely rapid succession which approaches simultaneity” and that during or immediately after inception, interprimordial growth creates a nearly “girdling primordium”. These discrepancies may be due to differences in light microscopy techniques employed by the investigators (none of which have the resolution provided by SEM) or by differences in the taxa examined.
Calyx -- Little variation was found in late stage and mature characteristics of the calices in representatives of the Malveae. All the calices are five-merous, green, serve as protective covers in the buds, and are fused basally, though the amount of fusion varied. An unusual feature of *Callirhoe involucrata* var. *involucrata* is that the sepals extend beyond the point of convergence in the bud, so that the lobes are distinct, divergent, and form a projection above the major portion of the bud. The inner bases of the sepals have glandular trichomes forming nectaries.

When it could be determined, the order of sepal initiation in representatives of this tribe was helical. Three of the taxa, *Malva neglecta*, *Anisodontea X hypomandarum*, and *Abutilon parishii*, did not have a sepal ring meristem. In *Hliamna remota*, this stage of development was not observed. The other taxa formed sepal ring meristems prior to initiation of sepal primordia, but these ring meristems were often poorly defined. In the other Malvaceous tribes I examined (Chs. 2, 3), most taxa had a sepal ring meristem, but at least one member of each tribe had independent initiation of the sepal primordia. Members of Gossypieae and Malvavisceae (with one exception) had helical sepal initiation. Representatives of the Hibisceae (with one exception) had simultaneous sepal initiation.

Similarly, Sattler (1973) did not see a sepal ring meristem in *Malva*. He reported the order of sepal initiation in *Alcea rosea* and *Malva neglecta* as a very rapid spiral that approaches simultaneity, and that subsequent interprimordial growth created a calyx tube. In *A. rosea*, he described the calyx as originally hexamerous with subsequent growth between two primordia resulting in a transformation to a pentamerous calyx. Payer (1857) characterized the sequence of sepal initiation in malvaceous buds that are
valvate as "quinconcial", i.e. helical or spiral. He also described sepal
initiation as either independent initiation with subsequent fusion or as
initiation by a common membrane. He did not, however, detail which type of
initiation was found in particular taxa.

**Pettals** -- Other than differences in color and perhaps petal shape
and size, the mature features of the corollas were very similar for
representative of the Malveae. All of the species have a five-merous corolla
which typically exceeds the calyx and the involucel, when present, in length.
The petals are basally adnate to the androecium, are not connate, have
paired basal ciliate tufts, and spread to form an open corolla in all taxa.
*Malva neglecta* is the only representative with an apical notch in each petal.
The overall shape of the flowers may vary among taxa, but other than to
determine if the flowers flared open or were tubular at maturity, this feature
was not examined in detail.

In all of the representatives of the Malveae as well as the other tribes
(Chs. 2, 3), the order of petal initiation is simultaneous. The petals are
positioned generally alternate to the sepals. Elongation of the petals is
delayed until after all of the common stamen primordia have initiated.

Previous researchers (as detailed in Chapter 3) have presented
several scenarios for the mode of petal inception in malvaceous flowers.
Payer (1857), van Heel (1966), Gore, 1935, Moncur (1981) described petal
inception on a petal-stamen ring meristem. Ault (1987) reported initiation of
petals prior to formation of a petal-stamen ring meristem. Sattler (1973)
characterized petals initiating independently with adnation to the androecium
occurring later. All of the taxa I examined in the Malveae as well as
representatives of the other large tribes (Chs. 2, 3) initiate a petal-stamen ring

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meristem prior to petal initiation. In all cases, the petals initiate on the outer
flank of the petal-stamen ring meristem. I saw no evidence of petals initiating
adjacent to the ring meristem and then being subsequently incorporated.

The time of inception of the petals was variable among taxa in
Malveae. The earliest occurs in *Lliamna remota* and *Abutilon parishii*, with
petal inception at the about same time that the ring meristem is divided
apically into five large mounded regions. Petal primordia appear during the
lateral partitioning of the upper portion of the ring meristem into ten mounded
common stamen regions in *Anisodontea x hypomandarum*, and after the
lateral partitioning in *Sida rhombifolia*. In the other four taxa, petals initiate
during various stages of centrifugal proliferation of common stamen
primordia. In the other tribes I examined, petal primordia initiate concurrently
or nearly so with the first staminal partitioning event, i.e. the first common
stamen primordia or mounds.

Previous literature is contradictory as to whether the petals or the
stamens initiate first in Malvaceae. Payer (1857) generalized that petals
appear before the stamens and he stated that Duchartre (1845) was probably
in error in saying that the stamens preceded the petals. Van Heel (1966)
concluded that in the Malveae, the petals arise when some of the stamen
primordia are present and in the other tribes petals seem to arise before any
stamen primordia. Sattler (1973) could not determine if the petals initiated
before, after, or simultaneously with the androecium in two members of
the Malveae. Several factors may account for the difficulty in determining
petal inception. First, there may have been confusion in distinguishing petal
primordia from common petal-stamen mounds (Ch. 3). Second, there seems
to be some conflict or lack of consistency in determining when the
androecium is initiated. Does the androecium begin with initiation of the five common mounds, with initiation of the ring meristem, or with partitioning events of the upper portion of the ring meristem? Also, initiation of the petal whorl and early development of the androecium occur very rapidly and critical stages may be easily overlooked. In addition, comparing the size of the petal primordia and the early common stamen primordia is not a reliable way to determine the sequence of inception since petal enlargement is retarded during stamen proliferation.

**Association between the corolla and the androecium**

There are several scenarios for early formation of the petal-stamen complexes, all of which are found in the Malveae. In the first scenario, a petal-stamen ring meristem forms first; this is usually evident by the pre-petal floral apex developing a peripheral raised rim around a central depression. Then five large mounded areas develop on the ring meristem in positions alternate to the sepals. At the base of each mound, a petal initiates and the raised portion becomes partitioned into common stamen primordia. With this scenario, there is no problem in labeling the initial raised rim as a petal-stamen ring meristem since both organ types initiate on it. In most cases, five mounds easily fit into the definition of common petal-stamen mounds or meristematic regions since they give rise to both organs. Both organ types may initiate on the mounded regions, result from partitioning of the regions, or at least initiate in the vicinity of the original mounds if the latter become less distinct with ring meristem enlargement. This type of initiation was found in most of the representative of the Malvavisceae and Hibisceae (Chs. 2, 3). A variation of this is found in *Abutilon parishii*, in which a ring meristem forms first, but then it appears as if the petal primordia and five large common
staminal mounds appear at the same time. It is unknown if common petal-stamen mounds develop between these events.

Another scenario involves the formation of the ring meristem concurrently with the five common mounded areas. Again, the terminology of petal-stamen ring meristem and common petal-stamen mounds would apply because of the fate of these structures. This type of development was found in *Malva neglecta, Sida rhombifolia,* and *Cienfuegosia ulmifolia* (Ch. 3).

With the third scenario, first a petal-stamen ring meristem forms. Then the apical portion of the meristem becomes partitioned into ten common stamen mounds with petal primordia initiating basally on the ring meristem during some stage of androecial partitioning. A stage with five common petal-stamen mounds or five common stamen mounds does not develop. This type of development occurs in *Anisodonteap x hypomandarum, Lavatera trimestris,* and possibly in *Abelmoschus manihot* (Chapter 3).

A fourth scenario has the five common mounded areas initiating first and then the formation of a raised peripheral rim and the central depression. The five common mounds may or may not be well defined and may or may not persist with formation of the ring structure. Since the five common mounded areas give rise to a structure that ultimately will produce both petals and stamens, the term common petal-stamen mounds or meristematic regions can be applied. The problem arises in what to call the mounded circular structure which follows. One could argue that intercalary growth between the five common petal-stamen mounds creates the mounded circular structure and thus it is not a true ring meristem. However, the common mounds that precede the ring structure are meristematic, not actual individual organ primordia. These mounds can be considered as changes in
the shape or form of the meristematic surface of the floral apex with no
discrete organ primordia produced during the change. Just because the ring
structure initially rises with an even surface, doesn't take away from the fact
that it is meristematic and will subsequently produce organ primordia. Thus,
if a ring meristem is defined as a circular mounded meristematic structure on
which primordia initiate, then this is a ring meristem. Since it produces both
petals and stamens, it is a petal-stamen ring meristem. This type of
development with mounded areas forming before the petal-stamen ring
meristem was found in Lliamna remota and Gossypium hirsutum (Ch. 3).
Determination of the order of development of the early petal-stamen
complexes in some species is complicated. In some taxa the early ring
meristem or the five common mounds are poorly defined and both develop
very quickly. In Hibiscus lasiocarpus (Ch. 3) the five common petal-stamen
mounds are so poorly defined and persist for such a short time that they can
easily be missed. Often there are gradations between these types of
initiation. For example, in Urena lobata (Ch. 2) and Radyera farragei (Ch. 3),
it is difficult to ascertain if they follow the first or the second scenario.

In most taxa, the stamen groups are opposite the petals, but there are
several exceptions to this. In Sida rhombifolia, an early stage of
development shows ten common stamen primordia in the first set, but rather
than the typical situation of an associated pair of these common stamen
primordia positioned on the same radius as a petal, in S. rhombifolia only
one of the associated pair is on the petal radius, while the other is alternate.
In the early stages of androecial development of Modiola caroliniana and
Malachra capitata (Ch. 2), only five common stamen mounds appear in the
first set and these are positioned alternate to the petals.
An interesting aspect of development is found in *M. caroliniana*. Five mounds develop alternate to the sepals prior to or at the same time as formation of the petal-stamen ring. With enlargement of the ring meristem, these original mounds become indistinct and five common stamen primordia arise on the ring meristem in positions interior and opposite the sepals. Even though the stamens arise in different positions relative to the original five mounds, the original mounds should still be considered as common petal-stamen mounds or meristematic mounds since they give rise to the petal-stamen ring meristem on which both organ types initiate.

Clearly there is a strong association between the corolla and the androecium in members of the Malvaceae. Both organ types initiate from a common floral structure, and this structure is a petal-stamen ring meristem. The common petal-stamen meristematic mounds can be considered as variations of the topography of the portion of the floral apex designated to form the petal-stamen ring meristem. Depending on the taxon, these common mounds may occur at any time during the formation of the petal-stamen ring meristem or may be absent. In some taxa, these common mounds result in the first partitioning of the ring meristem into sectorial regions. The fact that there are several different pathways to get formation of the petal-stamen ring meristem and many gradations between these, illustrates just how plastic the petal-stamen ring meristem is in Malvaceae.

**Androecium** — The merosity of stamens varies among taxa in the Malveae. *Sida rhombifolia*, *Modiola caroliniana*, and *Malva neglecta* have relatively low stamen numbers of less than 50. *Abutilon parishii*, *Anisodontea x hypomandarum*, and *Lavatera trimestris* are in the mid-range with stamen numbers generally between 60 and 100. Higher numbers of...
stamens (120 to 140) are found in *Callirhoe involucrata* and *Iliamna remotia*.
As few as five stamens have been reported in *Sidastrum* (Fryxell, 1997).
Stamen merosity was less variable in the other tribes. Representatives of the
Malvavisceae typically have low stamen numbers between 10 and 50 (Ch. 2).
Members of the Hibisceae and Gossypieae, with the exception of at least
*Kosteletzkya virginica*, generally have over a hundred stamens (Ch. 3). It
should be noted that stamen numbers may vary greatly within some taxa and
also among some literature references.

Some variation was found in the mature androecial characteristics for
representatives of the Malveae. All of the representative species have
androecial columns that are shorter than the corollas, although the height
ratio between the corollas and androecia vary among taxa. Filament
divergence is radial, but the position of filaments along the length of the
columns varies. In *Sida rhombifolia*, *Modiola caroliniana*, and *Abutilon parishii*
the filaments diverge only from the apical portion of the column.
Filaments diverge from the upper half or 1/3 of the columns in *Malva neglecta*, *Iliamna remotia*, *Lavatera trimestris*, and *Anisodonta x hypomandarum*. In *Callirhoe involucrata*, the filaments diverge along most of
the column. It is common in most representatives of this tribe to have
filaments that diverge in pairs, often partially fused, or sometimes singly.
In taxa with medium to large numbers of stamens, the filaments may be
clustered.

**Sterile androecial teeth** -- Members of this tribe characteristically
lack sterile teeth at the apex of the androecial column, whereas the other four
tribes of Malvaceae typically have five sterile teeth. The literature is
contradictory about the position of the sterile teeth as alternate to or opposite
the petals. Saunders (1936) emphasized that in no case is there an antesepalous whorl present in the androecium. In her view, all of the fertile stamens correspond to a single whorl of five antepetalous members, the primordia of which have undergone primary collateral splitting and have thus given rise to many half-stamens. The taxa examined by Saunders (1936) supposedly have teeth opposite the petals. Therefore, she believed that the teeth are terminations of the five fertile antepetalous members, and not the aborted sterile antesepalous whorl of the androecium as suggested by previous investigators. Even though most of the teeth are non-vascular, Saunders (1936) and Rao (1952) reported that some taxa have vascular bundles in the teeth, which result from prolongation of the vascular bundles of the antepetalous group of stamens. Rao (1952) also claimed that malvaceous flowers do not have any trace of an inner whorl of stamens, but his work only included four members of the Malvaceae. Payer (1857) and van Heel (1966) both reported that in some taxa, the sterile teeth are alternate to the petal radii, and in other taxa they are opposite the petal radii. My results are similar to Payer's and van Heel's in this matter. I found that in most cases, the sterile teeth are more or less in line with the stamen groups which are usually opposite the petal radii, i.e. one sterile tooth originates from the interior surface of each common petal-stamen region. There are, however, some exceptions to this. Three members of the Malvavisceae apparently do not have the teeth in line with the stamen groups (Ch. 2). One of these, *Malachra capitata*, has the stamen groups alternate to the petal radii; thus the sterile teeth are still opposite the petal radii. The other two taxa, *Pavonia strictiflora* and *Urena lobata*, have sterile teeth that are alternate to the petal radii. In the Gossypieae (Chapter 3) *Thespisia*
populnea has teeth that are in line with the stamen groups, but the stamen groups are on radii alternate to the petals, thus the sterile teeth are also alternate to the petal radii. In the Malveae, three taxa partially develop, then suppress, sterile teeth. In Callirhoe involucrata and Anisodontoea x hypomandarum, the small teeth are opposite the stamen groups and opposite the petal radii. Lavatera trimestris has young teeth alternate to the stamen groups and to the petal radii. The finding of some taxa that have stamen groups and/or sterile teeth that are alternate to the petal radii may refute Saunders' hypothesis, at least in reference to some taxa. Therefore, the sterile androecial teeth are extensions of the androecial tube and may be alternate or opposite with regard to the stamen groups and/or the petals.

In the other tribes which have sterile teeth, most taxa have five small spaces (areas of meristematic tissue not incorporated into staminal primordia) present on the inner surface of the petal-stamen ring meristem during early androecial partitioning events. These small spaces often elongate and contribute, at least in part, to the sterile teeth; but the teeth can form even if these spaces are absent (Chs. 2, 3). In the Malveae, Malva neglecta, Sida rhombifolia, and Modiola caroliniana have these small spaces on the young androecial ring meristem, but as the ring meristem elongates into a tube, this tissue does not develop into lobes but rather seems to be incorporated into the stamens. Therefore, having the extra meristematic spaces on the ring meristem doesn’t dictate that the teeth will form.

As previously mentioned, even taxa that lack the small spaces of unused tissue on the young androecial ring meristem can develop sterile teeth. These lobes appear to form from tissue on the interior surface of the ring meristem as it elongates into a tube. Callirhoe involucrata, Lavatera
*Trimestris*, and *Anisodontea x hypomandarum* develop minute to small sterile teeth during early elongation of the short androecial tube into a column, but these fail to fully develop and are completely absent at anthesis. This illustrates that sterile teeth appendages may be initiated but are suppressed in some members of the Malveae.

Are there any other differences in the formation of the androecial tube that account for the lack of mature sterile teeth in the Malveae? Regardless of whether teeth form, in all taxa the shape of the petal-stamen ring meristem is circular to pentagonal and the petals are typically alternate to the sepals. Merosity of stamens is not a factor since teeth are present in taxa that have low to high stamen numbers, and are absent in taxa with the same stamen numbers. There does not appear to be any correlation between the presence or absence of sterile teeth and whether the first set of common stamen primordia contains five, ten, or more members; whether the stamen groups are in line with or alternate to the petal radii; whether the androecial column is exserted or included; the overall height of the androecial column; or the pattern (scenario) of ring meristem formation. Based on casual observation, there does not appear to be any correlation between the presence or absence of sterile teeth and the size (total diameter and inside diameter) of the ring meristems at various stages. Elongation of the androecial tube occurs throughout partitioning events, during furcation of common stamen primordia, and during the process of stamen differentiation; there are not any noticeable delays or accelerations in elongation at various stages between taxa with sterile teeth and those without.

This SEM study was able to exclude several factors as possibly accounting for presence or absence of sterile androecial teeth. The exact
mechanism behind the formation of sterile teeth, however, is still elusive. More ontogenetic work is needed before the homology of the sterile teeth can be ascertained in the Malvaceae. Further research employing anatomical and genetic techniques may be needed to resolve this problem.

**Stamen proliferation** -- All of the representatives that I studied in Malveae, as well as Malvavisceae, Hibisceae, and Gossypieae (Chs. 2, 3), have a single whorl of stamens in the androecium. This does not imply that all the members of the whorl are equidistant from the central floral axis; i.e. this is not a "spatial whorl". The designation of a whorl in this case is based on the premise that all of the stamens or sets of stamens that make up the whorl originated from five common mounds, five common primordia, or/and a ring meristem. I did not observe a second whorl of androecial members initiating independently of the first whorl. There may, however, be exceptions to this in taxa that I have not examined. For example, *Sidalcea* is described with two series or phalanges of stamens (Fryxell, 1997). It should be noted that Fryxell's report is not based on developmental data. Often previous investigators (e.g. Payer, 1857; van Heel, 1966) used the terms series and whorl interchangeably with what I refer to as sets within a whorl, making direct comparisons difficult. An ontogenetic investigation of *Sidalcea* and perhaps some other taxa in Malvaceae is needed to discover if there are any true exceptions with more than one whorl of stamens in the androecium.

There are several variations in the early pattern of androecial partitioning. In most of the representatives of the Malveae, the apical portion of the petal-stamen ring meristem becomes partitioned into a set of ten common stamen mounds, with each associated pair of mounds interior and alternate with the sepals. Subsequent partitioning in a centrifugal direction...
creates ten radial rows of common stamen primordia, with five of the rows leading and the other five lagging. Generally, the common stamen primordia initiate in sets of five or ten with simultaneous initiation within each set. This kind of partitioning is typical of the Hibisceae and Gossypieae (Ch. 3). *Sida rhombifolia* differs at the stage with ten common stamen mounds in having only one of each associated pair alternate to the sepal radius, while the other member is opposite. It also only partially forms a second set of centrifugally initiated common stamen primordia (less than five primordia) and has such a low number of primordia that the term radial rows cannot be applied. 

*Modiola caroliniana* is unusual in having five common stamen primordia rather than ten on the surface of the petal-stamen ring meristem. These primordia are clearly positioned opposite the sepal radii, in positions alternate to the original common mounded areas that preceded ring meristem formation. Rather than becoming laterally partitioned, these common stamen primordia bifurcate laterally. A second set of common primordia initiates centrifugally, but these new primordia are off-center of the first set radii. The patterns of androecial partitioning found in *S. rhombifolia* and *M. caroliniana* are similar to patterns found in some members of the Malvavisceae (Ch. 2).

Furcation of common primordia, the actual spitting of primordia, differs from partitioning events, e.g. the initiation of primordia or common primordia from a common meristematic region (these terms are distinguished in Chs. 2, 3). Most representatives of the Malveae and of the Malvaceae typically have common stamen primordia that bifurcate, i.e. divide into two equal stamen primordia. There are several exceptions to this. *Iliamna remota* frequently has in the first and second sets (and occasionally in the outer sets) of the
androecium extra large common multistamen primordia which quadrifurcate to produce four equal stamen primordia. These large common multistamen primordia appear in positions where typically a lateral pair of bifurcating primordia would develop. It is important to note that quadrifurcation as described here is one furcation event (two simultaneous divisions) resulting in four primordia; not two consecutive bifurcations with the first event resulting in two common primordia and then the second resulting in a total of four primordia. In addition, some of the innermost common primordia in I. remota initiate as uneven pairs, with each pair consisting of a wide irregularly L-shaped primordium and a small primordium. The fate of these uneven pairs of primordial structures is not known for certain, but at early stages the larger of the pair appears to be asymmetrically two- or three-lobed as if it may bifurcate or trifurcate. The smaller remains unlobed as if it may not divide at all. Despite how frequently common multistamen primordia or odd-shaped common primordia occur during early stages of androecial development, almost all of the stamens in this taxon are bisporangiate. I also occasionally found extra large common primordia which form in place of a pair in Gossypium hirsutum (cotton), but the fate of these is uncertain (Ch. 3). Gore (1935) reported that in cotton the members of the ten rows of stamen primordia (except the bottom members) divide one or more times. In Alcea rosea, Sattler (1973) described the formation of elongated common primordia, which after several divisions gave rise to stamens. In some taxa in the Hibisceae and Gossypieae (Ch. 3) and the Malveae, the last androecial members to form on the column may not bifurcate. These latent members may form sterile filaments or bisporangiate anthers, I have not seen any tetrasporangiate anthers in these positions. Similarly, Ault (1987) described
in *Hibiscus acetosella* that the last-formed androecial members at the base of
the column may divide and develop into a stamen pair, develop into a single
stamen, or form a filament without sporangia. He did not say whether the
single stamens are bisporangiate or tetrasporangiate. In the Malvaviscaceae, I
found some bisporangiate stamens that arose by partitioning events and did
not result from any subsequent furcation processes (Ch. 2).

Since previous researchers (Payer, 1857; Saunders, 1936; van Heel,
1966) have attempted to attribute the formation of bisporangiate or "half-
anthers" to the bifurcation of common stamen primordia, the number of times
that the common primordia bifurcate is an important issue. If bifurcation
causes the reduction in sporangia from four to two per anther, then one might
assume that each common primordium should divide once, and only once.
Otherwise we might obtain anthers that are unisporangiate or
tetrasporangiate. Both Payer (1857) and van Heel (1966) described several
successive divisions without change in sporangia number; however, they did
not distinguish between partitioning and actual bifurcation. The large
common multistamen primordia of *Alcea rosea* (Sattler, 1973) and *lliamna
remota* produce bisporangiate, not unisporangiate, anthers; but it could be
argued that they result from ontogenetic fusion of two smaller common
primordia. However, the production of bisporangiate anthers from staminal
members that did not undergo any furcation challenge the idea that
bifurcation is responsible for the bisporangiate condition. Further evidence
comes from Ronse Decraene and Smets (1993), who reported in *Ricinus*
(Euphorbiaceae) that the process of splitting "can be repeated *ad infinitum.*"
Therefore, bifurcation does not appear to correlate with the
bisporangiate condition. As described in Chapters 2 and 3, the processes of furcation and partitioning are simply a means of proliferation of the bisporangiate condition.

The direction of early bifurcation (or furcation) is variable among representatives in the Malveae. In most taxa, the innermost sets of common stamen primordia bifurcate in a radial to radial-oblique direction. In * Modiola caroliniana*, *Callihroe involucrata*, and *Iliamna remota* the inner sets of common stamen primordia bifurcate in a lateral to lateral-oblique direction. The direction of these bifurcations appears to be related to the number of members in the inner set and the size of the androecial tube (inside diameter) at the time the common primordia are broadening. Crowded conditions result in the bifurcation in a more radial direction. In the outer sets where crowding is less of a problem, the common stamen primordia in all the taxa bifurcate in a lateral to oblique direction.

**Gynoecium** -- There is some diversity in mature characteristics of the gynoecium. Merosity of the carpels varies among and within species. The numbers range from six to 25 in the representative taxa studied. It should be noted that some members of the Malveae, in particular members formerly placed in a separate tribe known as Malopeae, are described with much higher carpel merosities (Kearney, 1951; Hutchinson, 1967; Bates, 1968; Endress, 1981; van Heel, 1995). In all the taxa in my study, the gynoecia are shorter than the corollas, although the amount of inclusion differs. In most taxa, the gynoecia are 1/2 the height of the corollas or less. *Callirhoe involucrata* is the exception with the gynoecium 2/3 as tall as the corolla. The gynoecia also extend beyond the androecia, although in some species they extend only marginally, and in others the styles are...
long-exserted. Two stigma types are present in the representative taxa. Most have capitate stigmas; but three species, *Malva neglecta*, *C. involucrata*, and *Lavatera trimestris*, have introrsely decurrent stigmas. Another variable feature is the number of ovules per locule. One ovule per locule is typical of most of the representative taxa studied; the exceptions are *Modiola caroliniana* with two ovules per locule, *Liamna remota* with two to four ovules per locule, and *Abutilon parishii* with three ovules per locule. As many as seven ovules per locule have been reported in *Bakeridesia* (Fryxell, 1997).

Several features of the gynoecium are consistent among all taxa examined. In the gynoecium, all of the carpels typically form fertile locules. An apical residuum remains in the center of the young gynoecial whorl. The mature ovary is syncarpous, superior, segmented, and has axile placentation. Styles are fused basally into a column and divergent apically.

One controversy concerning carpel initiation in this tribe is whether or not they initiate as a single whorl. Thus it becomes necessary to define a whorl. Typically, a whorl is defined as an arrangement of similar parts in a circle around a point on an axis. All the representative Malveae taxa in my study have carpels initiated in a single spatial whorl in each gynoecium. Similarly, members of the Malveae (excluding the former Malopeae genera) are depicted with carpels in a single whorl by Payer (1857), Kearney (1951), Hutchinson (1967), and Sattler (1973). Three genera, *Palaua*, *Malope*, and *Kitaibelia*, were placed into a separate tribe called Malopeae by Kearney (1951) and Hutchinson (1967) and described as having carpels arranged in two or more superposed whorls. These genera are now incorporated into the Malveae by Bates (1968) and Bates and Blanchard (1970). Payer (1857) and van Heel (1995) depicted young gynoecial members as arranged in a
pentagon in *Kitaibelidia* and *Malope*. Van Heel (1995) described the young carpels in these taxa as arranged “around the floral apex in a whorl with five lower, outer curves and five upper, inner curves” in a way that he describes as a “continuous” or “conical wave-line”. Obviously, in these genera the spatial patterns of carpel initiation are more complex and do not easily fit into the definition of a single spacial whorl unless the definition is expanded to cover other geometric shapes such as pentagons. Thus, the taxa in Malveae may initiate the carpels in a single spacial whorl or (as is the case in Malopeae genera) by more complex patterns which may position the carpels in several spacial whorls. In the Gossypieae and Hibisceae (Ch. 3) the carpels initiate in a single spacial whorl. An unusual situation is found in the Malvavisceae, in which the carpels initiate as two sets of five within the same spacial whorl (Ch. 2).

In all of the taxa I examined in this tribe, the order of carpel initiation was simultaneous. Some taxa, such as *Modiola caroliniana* and *Iliaamna remotia* form a low carpel ring meristem prior to initiation of carpel primordia. In *Lavatera trimestris*, a low raised structure with a slightly uneven surface develops prior to discrete carpel primordia. At this stage, interpretation of this structure is subjective as to whether it is a low carpel ring meristem with the first indications of carpel primordia or if it is a whorl of connate carpel primordia. I tend to favor the ring meristem interpretation since the carpel primordia are so poorly defined on a continuously raised ring. In the other five representatives of this tribe, the gynoecium appears as a ring of connate carpel primordia, it is unknown if a ring meristem precedes initiation of the carpel primordia. Determination of a carpel ring meristem and ontogenetic carpel connation in this tribe is difficult for several reasons. First, when a ring
meristem is present, it is often low and poorly defined. Secondly, the carpel primordia may initiate on the ring meristem without any obvious increase in size or definition of the ring meristem, which suggests that carpels form rapidly after the ring meristem and that critical stages showing formation of the ring meristem may be easily missed. Thirdly, some of the members of this tribe have such high carpel numbers that the carpel primordia may appear to be connate due to crowding. Carpel ring meristems are not unique to this tribe. I found that low carpel ring meristems are present in most members of the Gossypieae but appeared to be lacking in the Hibisceae and Malvavisceae (Chs. 2, 3).

Payer (1857) did not report a carpel ring meristem in any of the malvaceous taxa he examined. In Kitaibel\textit{ia} and \textit{Malope}, he described the formation of five gynoecial humps (common meristematic mounds) on which carpel primordia initiate consecutively. Similarly, Endress (1981) stated that in \textit{Kitaibel\textit{ia}} the gynoecium initiates as five primordia which each subdivide into a row of about 10 secondary primordia. In contrast, van Heel (1995) depicted that in \textit{Kitaibel\textit{ia}} and \textit{Malope}, the gynoecium first arises as a continuous girdling meristem. Subsequently the carpel primordia appear simultaneously. Sattler (1973) described that in \textit{Alcea rosea} the gynoecium initiates first as a rim, which immediately after its inception, becomes undulated with the initiation of gynoecial primordia. In \textit{Malva neglecta}, Sattler (1973) stated that the gynoecium initiates as five primary primordia that subsequently form an almost even ridge by interprimordial growth, and then each primary primordium usually forms three secondary gynoecial primordia. In regard to the issue of common gynoecial primordia, I did not observe a stage with five common gynoecial primordia in \textit{M. neglecta}, and I
did not include members of the former Malopeae in this study. With respect to the discrepancy about whether a carpel ring meristem forms, as previously mentioned not all taxa form ring meristems and in taxa that do form ring meristems the critical stages are easily missed, especially without the aid of SEM.

**Pollen and fruit** -- Some variation was found in the schizocarps of representatives of the Malveae. Most taxa have fruits that are wider than tall; *Abutilon parishii* is the exception with fruits that are taller than, or equal to, the width. Typically the schizocarps are indehiscent; however, *Lliamna remota* and *A. parishii* have dehiscent fruits and *Modiola caroliniana* has fruits that are incompletely dehiscent. The mericarps in *Malva neglecta* are covered with very short trichomes and surround a very prominent central disk. *Lavatera trimestris* has a large cap over the laterally ribbed mericarps. Several of the taxa have fruits with various appendages: *Sida rhombifolia* has two spines per mericarp, *M. caroliniana* has two spines per mericarp and long trichomes, *A. parishii* has one spine per mericarp that divides upon dehiscence, *Callirhoe involucrata* has a short blunt apical lobe on each mericarp, *Anisodon* *t*ea *X hypomandarum* has two blunt apical lobes per mericarp, and *I. remota* has long trichomes. All of the taxa have persistent sepals and bractlets, except *S. rhombifolia* and *Abutilon parishii* which lack bractlets. In most, these organs generally point in an upward direction around the fruit. In *C. involucrata* the sepals tend to be oriented in an outward direction and the bractlets are directed more or less downward.

One feature that was pointed out by Kearney (1951), Bates (1969), and Dorr (1990) is the presence of an endoglossum in some species. Two of the taxa I examined, *Modiola caroliniana* and *Callirhoe involucrata* var.
involucrata, have an endoglossum. In the case of M. caroliniana it divides each carpel into two chambers with an ovule in each. In C. involucrata it divides each carpel into a one-ovulate lower chamber and an upper sterile chamber. Bates (1969) presumed that some species of Callirhoe, Urocarpidium, and Malvastrum, which have uniovulate carpels and endoglossa, are the end product of a reduction sequence from pluriovulate carpels with endoglossa to uniovulate carpels with retained endoglossa.

Pollen grains in this tribe are typically spheroidal (or spherical) and echinate. Iliamna remota and Abutilon parishii have pollen that is spheroidal to suboblate in shape. Anisodontea X hypomandarum, I. remota, and A. parishii have zonocolporate apertures, whereas Lavatera trimestris, Malva neglecta, and Callirhoe involucrata var. involucrata, have various arrangements of porate apertures. Aperture type was not determined for the other two representative taxa.

Analysis of characteristics and placement of certain taxa --
One of the major characteristic that has been used in the past to distinguish members of the Malveae is the lack of sterile teeth at the apex of the androecium (Fryxell, 1975, 1988). My findings verify that the sterile teeth are lacking at maturity; however, some taxa in the tribe may initiate but suppress teeth. Therefore, I believe that the importance of this character may have been overemphasized. The other distinguishing morphological characters, mainly pertaining to the gynoecium, are supported by the findings of the current work. Members of this tribe have schizocarpic fruits with a one to one ratio of stigmas to mericarps or locules, the many to numerous styles per gynoecium are apically free, and the locules may be uniovulate or pluriovulate. Some diagnostic features (such as embryo characteristics and
the lack of gossypol glands, involucellar nectaries, and foliar nectaries) were not targeted as part of this research. However, no obvious deviations were noted. Many of the distinguishing characteristics are shared with members of other tribes, but not the combination of all of these. In previous research (Chs. 2, 3), stamen merosity appeared to be a useful feature in characterizing the Malvavisceae, Hibisceae, and Gossypieae; but in the Malveae the stamen merosity ranged from relatively few to numerous. Many floral morphological features (such as carpel merosity, petal color, presence or absence of involucels, jointed or nonjointed pedicels, height ratios of various organ types, shape of bractlets, pattern of filament divergence, stigma types, and details of the pollen grains and fruits) were useful in distinguishing among genera in the tribe.

Many variations in ontogenetic characters were found among taxa in the Malveae. All four scenarios for formation of the petal-stamen ring meristem were present among the representative taxa. As previously mentioned, some taxa may at least initiate androecial sterile teeth. Other features that vary among the taxa include: presence or absence of ring meristems in the bractlet, sepal, and carpel whorls, presence or absence of connation among the involucellar bracts, amount of fusion in the calices, timing of petal inception, presence or absence of common petal-stamen mounds, position of petals relative to stamen groups, early partitioning events in the androecia, and direction of furcation of inner common stamen primordia. The wide range of ontogenetic characters found in such a limited sampling of the Malveae illustrates the diversity of this taxonomic group within the Malvaceae.
Not enough taxa were examined in this tribe to make any conclusions regarding placement of certain taxa into alliances. *Modiola caroliniana* stands apart from the other taxa with respect to partitioning of the androecium. In this species, there were only five common stamen primordia in the innermost set rather than ten, the stamen groups are positioned on the same radius as the sepals rather than alternate, and the stamen groups were not in line with the petals. A similar situation is present in the androecium of *Malachra capitata* in the Malvaceae (Ch. 2).

**Characterization of the tribe** — The ensuing ontogenetic and developmental characterization of the Malveae is preliminary. Only a limited number of taxa could be examined in this research project, and it should be noted that the Malveae is very large with approximately 70 genera (Table 4.2) and that many of these genera contain numerous species (Kearney, 1951; Hutchinson, 1967; Fryxell, 1988). As more taxa are examined in this tribe the boundaries will certainly have to be modified.

In the Malveae, flowers of representative taxa typically have bractlets, or less commonly lack them. When present, the involucels are three to many-merous and distinct; less frequently they are basally fused. In most cases, the involucel subtends the calyx, however some variation in position may occur. Bractlet primordia initiate helically, usually without a bractlet ring meristem. The calyx is five merous, basally fused, and exceeds the involucel (when present) in length. Initiation of sepals is generally helical and may or may not involve a sepal ring meristem. The corolla exceeds the calyx in length and flares to form an open flower. The petals are not connate but are basally adnate to the androecium. The five petals initiate simultaneously at the base of a petal-stamen ring meristem. Common petal-stamen mounds
may develop prior to, during, or after formation of the petal-stamen ring meristem or they may not develop at all. Time of petal initiation may occur early with the first partitioning event of the upper androecial portion of the ring meristem or occur much later with the centrifugal proliferation of common stamen primordia. The petals are positioned alternate to the sepals. Petal elongation is delayed during stamen proliferation. The androecium consists of as few as five stamens to numerous (120 -140) stamens, with numbers varying among and within species. The innermost set of common stamen primordia may contain five or ten members. After initiation of the first set of common stamen primordia, the proliferation of common stamen primordia proceeds in a centrifugal direction. In taxa with large numbers of stamens, the common stamen primordia are arranged in ten radial rows, usually five leading and five lagging radial rows. The innermost set or sets of common stamen primordia may bifurcate in a radial, oblique, or lateral direction. The common primordia in the outer sets bifurcate in a lateral to oblique direction. Some taxa may have large, common multistamen primordia which furcate to produce more than two stamen primordia. The stamens are produced in five regions or groups which are usually opposite the petals, some exceptions to this are found. The filaments may diverge singly, in pairs, in partially fused pairs, or in groups from the androecial column. Filament divergence is radial and may range from only apical to nearly throughout the length of the column. Although in some taxa sterile teeth may be initiated, at maturity the apex of the androecial column completely lacks sterile teeth. The pollen is spheroidal to spheroidal-suboblate in shape, is echinate, and has either porate or colporate apertures. The numbers of apertures appears to vary greatly among taxa; this is verified by actual counts made by Christensen.
The gynoecium is composed of six to numerous carpels, with the numbers varying among and within species. All of the carpels are fertile. Each locule may contain one to many ovules depending on the species. The ovary is syncarpous, superior, and has axile placentation. The styles are basally fused into a column and divergent apically. Stigmas are capitate or introrsely decurrent and there is a one-to-one ratio of stigmas to mericarps. The carpels initiate as a connate whorl and in some taxa may initiate on a carpel ring meristem. All of the carpel primordia of the gynoecium initiate simultaneously in a single spacial whorl (except perhaps in Malopeae). An apical residuum remains in the center of the young gynoecium. The fruit type is a schizocarp that may be indehiscent, dehiscent, or partially dehiscent. The fruits have obvious segmentation and are, with some exceptions, generally wider than tall with persistent sepals and bractlets. The surface of the fruits may contain a central disk, a variety of trichomes, and/or appendages such as lobes, spines, or caps.

**Summary** -- The use of SEM to look at floral ontogeny in this and previous chapters has been a valuable tool to show the ubiquity of certain floral features among members of the Malvaceae. For example, all the representative taxa have a petal-stamen ring meristem resulting in the ontogenetic adnation of the petals to the androecium and the connation of the androecial members. Petal elongation is delayed during stamen proliferation. The involucellar bractlets initiate on the floral apex whereas bracts or leaves initiate adjacent to the floral apex. There appears to be a transition from helical initiation of organs in the outer organ whorl or whorls to simultaneous initiation in the inner organ whorls or organ sets. Ring meristems, when they occur in the bractlet, sepal, or carpel whorls tend to be
ambiguous. Also, common stamen primordia are prevalent in the young androecia.

This technique of examining ontogenetic series has also clarified development and homology of some of the unusual floral structures found in malvaceous flowers (see also Chapters 2 and 3). For example, it has been illustrated that there are several ontogenetic pathways to the formation of the petal-stamen ring meristem, and that there is some variation in the partitioning and furcation events that occur in the androecium. The current work has refuted the idea that bifurcation and partitioning events are the likely causes of the bisporangiate condition. It has been shown that there are several pathways to connation in the outer organ whorls and that presence of a ring meristem doesn’t dictate that connation will be present at maturity. In some taxa, suppressed organs such as bractlets and sterile androecial teeth have been elucidated. Although the exact mechanism behind the formation of sterile teeth was not ascertained, several factors were identified as sometimes contributing, and some were ruled out as causal. In the Malvavisceae (Ch. 2), the initiation pattern, position, and subsequent fate of the sterile carpels was revealed. In addition, several unusual features have been shown such as the common bractlet primordia that occur in \textit{Radyera farragei} and the displacement of bractlets in some taxa.

Ontogenetic research has added insight into the systematics of the Malvaceae. Some ontogenetic characters may be valuable in distinguishing among the tribes and among certain genera. It was not determined if they could be of value in clarifying classification at the species level. The evolutionary aspects of ontogenetic characters will be explored in Chapter 6 with a cladistic analysis.
LITERATURE CITED


CHAPTER 5
FLORAL DEVELOPMENT IN OUTGROUP TAXA STERCULIA CERAMICA AND HERRANIA SP. (STERCULIACEAE) AND IN PACHIRA AQUATICA (BOMBACACEAE) WITH COMPARISON TO MALVACEAE

INTRODUCTION

Bombacaceae and Sterculiaceae (along with Malvaceae, Tiliaceae, and Elaeocarpaceae) are in the order Malvales (Cronquist, 1981, 1988). Little previous floral developmental research, with the exception of *Theobroma* (Sterculiaceae), has been done for members of these two families using scanning electron microscopy (SEM). Therefore, a focus of this research will be to examine the floral ontogeny and development of two representatives of Sterculiaceae (*Sterculia ceramic* and *Herrania* sp.) and one representative of Bombacaceae (*Pachira aquatica*) using SEM.

Information obtained about floral ontogeny and development will hopefully provide insight into the formation of floral structures in these taxa, provide a basis for characterizing floral development in each family, help to clarify floral distinctions between these two families, and will provide comparative data for a larger study of the Malvaceae. Ultimately, these taxa will be used as outgroups in a cladistic analysis of Malvaceae.

Sterculiaceae includes the economically important genera *Cola* and *Theobroma* (Cocoa) as well as several ornamentals. Most estimates place between 60 and 65 genera in Sterculiaceae. *Sterculia* and *Dombeya* are the largest genera, with an estimated 300 or more species in each. Members of this family are typically tropical and subtropical trees or shrubs, sometimes
lianas or herbs. The flowers are mostly in complex inflorescences or (more rarely) solitary, and are bisexual or unisexual (sometimes both on the same plant). They often have an epicalyx (involucel or bractlets). The flowers have a three- to five-merous valvate calyx that is usually fused basally. Multicellular glandular hairs form a nectary at the base of the sepals. The corolla may be lacking or three- to five-merous. The petals are not connate, but may be adnate basally to the androecium and may be hooded. The stamens appear to be in two cycles or whorls, of which one whorl of five is commonly reduced to staminodes or suppressed. The other whorl includes normal anthers and is either five-merous or in five bundles of two, three, or more members. The filaments may be unfused, but are usually connate into a tube. Anthers are tetrasporangiate and dithecal with pollen sacs that open mostly by longitudinal slits or, more rarely, by apical pores. The pollen grains are tricolporate and smooth or reticulate to pantoporate and spinulose. The gynoecium is typically two- to 12-merous, rarely it has only one or up to 60 carpels. The ovary has as many locules as carpels. It may be syncarpous with unfused or connate styles, consists of distinct carpel bases with temporarily fused styles, or consists of completely distinct carpels. There are two to many (rarely one) ovules per carpel in axile, marginal, or deeply intruded parietal placentation. The fruit is a dry follicle, cluster of follicles, capsule, schizocarp, or sometimes fleshy and berry-like. It may be dehiscent or indehiscent (Benson, 1957; Cronquist 1968, 1981; Heywood, 1985; Gentry, 1993). Morphological descriptions of the genus Sterculia are available in Baillon (1875), Bailey (1935), and Gentry (1993). Herrania (a segregate of Theobroma) consists of 17 species (Gentry, 1993), which have
been described mostly in obscure references. The genus is briefly described in Baillon (1875), Cuatrecasas (1964), and Gentry (1993).

In Bombacaceae, some of the better known genera include *Ochroma* (Balsa), *Adansonia* (Baobab), *Durio* (Durian fruit), *Bombax* (Silk-cotton tree), and *Ceiba* (Kapok-tree). The family consists of between 20 and 30 genera. Members of the Bombacaceae are tropical trees and are often very large. The flowers are bisexual and usually large and showy. Flowers may be solitary or in clusters, and they occur in leaf axils, opposite a leaf, or in cauliflorous clusters. An epicalyx is often present. The calyx is five-merous with valvate sepals that are unfused or connate. A glandular trichomatous nectary is present at each sepal base. The five petals (when present) are unfused and convolute. The androecium has five to numerous stamens and/or staminodes that are adnate to the petal bases and often connate by their filaments into five to 15 fascicles (groups) or into a tube that separates into five to 15 fascicles. The anthers are monothecal (bisporangiate) and open by longitudinal slits. Pollen is commonly oblate and angular in outline with a smooth, reticulate-rugose, or (rarely) spinulose surface texture. Pollen apertures are tricolpate, tricolporate, triporate, or pantoporate. The gynoecium is a syncarpous ovary with two to five (up to eight) carpels and partially or completely fused styles. Carpel merosity equals locule number and placentation is axile. Each locule may contain two or more ovules. The fruit is a loculicidal capsule, or rarely fleshy and indehiscent (Benson, 1957; Cronquist, 1968, 1981; Heywood, 1985; Gentry, 1993). *Pachira* is a small genus with only two species (Gentry, 1993). Morphological descriptions of the genus *Pachira* have been provided by Baillon (1875) and Gentry (1993) and for the species *P. aquatica* by Bailey (1935) and Robyns (1964).
Most previous floral development studies that have focused on members of Sterculiaceae and Bombacaceae did not include complete ontogenetic series. Light microscopy techniques were used by Rao (1952) to look at the vasculature of one species of Bombacaceae and seven of Sterculiaceae, and by Davis and Mariamma (1965) to examine stamen types in *Bombax ceiba* (Bombacaceae). Light microscopy was employed by van Heel (1966) primarily to analyze vascular and developmental aspects of the androecium in numerous taxa in these families; often, however, the very early stages of androecial development were not observed. The three genera chosen for my research were included in van Heel's study. SEM was used to examine the gynoecium in *Brachychiton* (Sterculiaceae) (Jenny, 1983; Endress, Jenny, and Fallen, 1983) and in *Firmiana* (Sterculiaceae) (Jenny, 1983). Two taxa of Bombacaceae (*Matisia cordata* and *Durio zibethinus*) and one of Sterculiaceae (*Theobroma cacao*) were viewed by Moncur (1988) with SEM, but he did not provide complete ontogenetic series or describe the ontogeny. A complete floral ontogeny with SEM of one species, *Theobroma cacao*, was done by Bayer and Hoppe (1990). With so few species studied thoroughly, a detailed ontogenetic study is needed to determine the complex patterns of organ initiation in flowers of selected species from these two families.

**MATERIALS AND METHODS**

Floral material of three taxa was collected from various sources (Table 5.1). When possible, herbarium vouchers were made and retained by the author. Floral buds of various developmental stages were collected and fixed in formalin-acetic acid-alcohol (FAA). Prior to dissection, buds were transferred through two to four changes of 95% ethanol, then dissected in
TABLE 5.1. Sources of Sterculiaceae and Bombacaceae plant material and voucher information for taxa examined in this floral study.

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<tr>
<th>Taxon</th>
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<th>Source, collector, and date</th>
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<td><strong>Sterculiaceae</strong></td>
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<td><strong>Bombacaceae</strong></td>
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95% ethanol. Material was dehydrated in 100% ethanol and critical point
dried in a Denton DCP-1 with liquid CO2. Specimens were mounted on
aluminum stubs with Avery press-on Spot-O-Glue and sputter-coated with
gold-palladium in an Edwards S-150 apparatus. Micrographs were taken
using a Cambridge S-260 scanning electron microscope at 15 kV and spot
size 6. Kodak Tri-X (TXT 4164) sheet film was used.

Most stages of floral initiation and development were obtained using
SEM techniques. Some late stage floral characters were obtained by
examination of herbarium vouchers and FAA-ethanol preserved material with
various dissecting and light microscopes. In some instances, literature was
consulted to verify and complete mature floral descriptions.

Terminology — Several terms that are used frequently in the
following text need to be defined. In much of the previous literature, the terms
set, whorl, tier, and series are used ambiguously in reference to the
androecium and gynoecium in Malvales, thus leading to confusion when one
tries to compare very complex floral structures. I have opted to use only the
terms set and whorl and have tried to clarify the meaning of each. Steen
(1971) defines a whorl as a group of three or more similar structures, such as
leaves, that arise at one point and are arranged in the form of a circle; a
verticil. To this I would add that the members of a whorl initiate from similar
areas or common areas (common primordia, common mounds, or a ring
meristem) on the floral apex. Usually one whorl differs from another in
relative position in the flower. For instance, all of the stamens that compose
one whorl would be generally opposite the petals, whereas those of another
whorl would be alternate with the petals. This may not always apply if ring
meristems are producing the whorls. In addition, one whorl is usually more
interior than another; but, there are some exceptions to this. For example, in the Malvavisceae tribe (Malvaceae) the two sets (or in this case whorls) of carpels initiate alternately and equidistant from the central floral axis; i.e. one set is not interior to the other. So, for lack of a better term, the two sets (whorls) of carpels share the same spatial whorl. A set of primordia (as defined in Ch. 2) consists of identical (same type) primordia that have initiated at the same time in the same relative positions. One whorl may consist of one set or several sets of primordia. For example, the androecium in *Malvaviscus arboreus* consists of one stamen whorl with five, five-merous sets of stamens (Ch. 2). A ring meristem is a meristematic rim or ring of tissue on the floral apex that is set apart from the rest of the floral apex (either by a trough separating it from the remaining raised central portion of the apex or by a central depression in the remaining floral apex). This ring meristem is capable of producing a whorl or whorls of organs. An androgynophore is defined by Radford et al. (1974) as the stipe or column on which stamens and carpels are borne. Other terms pertaining to floral features have been defined in Chapter 2 or as needed in this chapter.

RESULTS

*Sterculia ceramic* (Sterculiaceae) -- Organography -- The plant is a large tree with very small tubular flowers arranged in typically large inflorescences. The flower lacks an involucel and corolla. The calyx consists of four (seldom three or five) cream-colored connate sepals. The androecium consists of numerous stamens that are united into a column with sessile anthers. The gynoecium has five unfused carpels that produce a group of follicles.
Initiation and early development of the calyx — Many to numerous flowers initiate in each inflorescence (Figs. 5.1, 5.2). Young inflorescences are usually packed tightly with various sizes of flower buds (Figs. 5.1, 5.2); but with elongation of the pedicels, the inflorescences become very much expanded. The pedicels are jointed a short distance below, or sometimes at, the receptacle bases (Fig. 5.1). Typically four sepal primordia initiate helically on the periphery of a short-stalked floral apex (Figs. 5.3 - 5.7). A ring meristem is not involved in sepal initiation (Fig. 5.3). Occasionally, sepal number is three (Fig. 5.2) or five (Figs. 5.1, 5.7). As the sepal primordia differentiate and enlarge, they form a protective dome over the rest of the floral apex and become fused basally (Figs. 5.6, 5.8). In young buds, the lobes of individual sepals are easily discernable at the apex (Figs. 5.1, 5.2, 5.7).

Initiation and early development of the androecium — The apex to the interior of the sepals is initially convex (Figs. 5.5 - 5.8). While the sepals are forming a protective dome, the floral apex becomes broader, flatter, and somewhat pentagonal in outline, and it may develop appression marks from the sepals (Fig. 5.8). Then the upper surface of the floral apex becomes undulated as many poorly defined mounds appear (Fig. 5.9). With further development, the first ten staminal primordia become apparent (Fig. 5.10). During initiation of these ten androecial primordia, there is no surface evidence of any androecial ring meristem or of petal primordia. Five of the staminal primordia, designated the outer whorl, are slightly exterior and alternate to the other five staminal primordia, the inner stamen whorl. Both of these whorls initiate at the same time, and the order of initiation within each is simultaneous. Next, each member of the outer whorl of common stamen
primordia partitions laterally into two mounds (Figs. 5.11, 5.12). Subsequently, each inner stamen primordium begins to differentiate; this is apparent by the base narrowing and the apex broadening and becoming two-lobed (Figs. 5.13 - 5.16). As the androecium elongates basally into a tube (actually a common androecial and gynoecial platform), the outer stamen whorl develops into five common irregularly-shaped meristematic structures (pads) which are positioned along the exterior sides of the tube. At first, each outer androecial meristematic pad has just the two earlier-formed mounds (stamen primordia) near the apex (Fig. 5.13); but with further development, each meristematic pad initiates many (generally six to nine) stamen primordia (Figs. 5.14 - 5.16). With continued elongation of the androecium into a column, each member of the inner and outer stamen whorls develops a sessile tetrasporangiate anther with more or less parallel thecae (Figs. 5.18 - 5.20, 5.22). Anther differentiation proceeds from the top of the column downward (Fig. 5.18). The inner stamens are oriented upward whereas the outer stamens face outward on the column (Figs. 5.18, 5.19, 5.22).

**Initiation and early development of the gynoecium** -- The floral apex to the interior of the androecium becomes pentagonal in outline, with the sides on the inner stamen radii (Figs. 5.11, 5.12). The five carpel primordia initiate in positions alternate to the inner stamen whorl members, i.e. one carpel in each corner of the pentagon (Figs. 5.12, 5.13). Carpel initiation is simultaneous and no ring meristem is involved. The gynoecium develops on an elevated platform that is continuous with the lower portion of the androecial tube (Figs. 5.13, 5.15, 5.19). At first, the gynoecium expands radially to become star-shaped, and each carpel primordium develops an
adaxial (radial) groove (Fig. 5.14). With further development, the grooves deepen into locular crevices, and some or all of the carpels become oriented more vertically (Figs. 5.17, 5.19). As the carpel tips elongate into short styles, some or all of the young styles may protrude outward between the bases of the inner stamens (Figs. 5.18, 5.19). Each carpel develops a fertile locule with two or three ovules (Figs. 5.20, 5.21).

Mid and late stage floral development — The shape of the flower buds changes from ovate or depressed obovate (Figs. 5.1, 5.2, 5.20) to elliptic (Fig. 5.22). The calyx becomes very thick, and develops glandular trichomes on the inner base and in dense mats on the inner apical lobes (Fig. 5.22). At maturity, the calyx is tubular except at the very apex, where the sepal lobes flare distally (Fig. 5.24).

After all of the anthers have differentiated, the androecium elongates basally so that the anthers are presented on the upper and middle levels of the column and the lower level is bare (Figs. 5.23, 5.24). The mature androecium is included in the calyx tube (Fig. 5.24). The anthers dehisce by longitudinal slits at the sporangial sutures and both whorls of stamens produce pollen (Fig. 5.24). Pollen is spheroidal, tricolporate, and has a raised reticulate surface texture (Fig. 5.25).

The carpels are elevated on a common androecial and gynoecial column, i.e. androgynophore (Fig. 5.23). In the flowers I examined, the gynoecium never exceeded the androecium in height (Figs. 5.20, 5.23, 5.24). At the time of anther dehiscence, the carpels are small, included in the androecium, and do not have an obvious stigmatic surface on the styles.

The fruits are very large relative to the size of the flowers. Each fertile flower typically produces five large brown follicles which radiate outward.
Figs. 5.1 - 5.7. Sterculia ceramica, young inflorescences and various stages of calyx initiation and early development. Bars = 500 µm in 5.1, = 1 mm in 5.2, = 50 µm in 5.3 - 5.5, = 100 µm in 5.6 and 5.7. 5.1. Small portion of an inflorescence with flower buds at various stages of sepal (S) initiation and development. Sepal merosity varies from three to five, with four most typical. The members of the calyx are not always equal in size. The pedicels (pd) are articulated near or sometimes at the junctions to the receptacles (two shown at arrows). 5.2. Less dense cluster of flower buds. There is a bud with only three sepals. Calyx members are not always equal in size (*). Floral bracts (B) subtend the base of the inflorescence (or this part of an inflorescence). 5.3. Floral apex that has one sepal primordium present and shows early initiation of another (at arrow). No sepal ring meristem is present. The floral apex is on a short pedicel (stalk). 5.4. Floral bud with three helically initiated sepals (sequence of initiation shown with numbers). 5.5. Floral bud with four helically initiated sepals (sequence of initiation shown with numbers). The remaining floral apex (A) is convex. 5.6. Four sepal primordia (only one labeled) which have enlarged slightly. 5.7. Floral buds at various stages. The largest bud in the upper right of the micrograph has four sepals forming a protective dome over the interior portion of the flower. The bud to the left has a three-merous calyx. The bud at the bottom center has initiated one sepal primordium.
Figs. 5.8. - 5.13. *Sterculia camerica*, initiation of the androecium. Bars = 100 μm. 5.8. Pre-androecial apex. The sepals have fused basally; this is evident by the continuous calyx scar. The apex to the interior of the calyx has appression marks from the sepals. 5.9. Initiation of the inner and outer stamen whorls is evident by the numerous small staminal mounds on the apex to the interior of the calyx. No androecial ring meristem is present. 5.10. Five inner stamen primordia (ISt, only two labeled) and five outer stamen primordia (OST, only two labeled) are present. The order of initiation within each of these whorls is simultaneous. The outer stamen whorl members are exterior and alternate to the interior stamen whorl members. 5.11. Each of the five original outer common stamen primordia has a radial groove, thus partitioning each into two mounds. The remaining floral apex is pentagonal in outline and slightly convex. 5.12. Simultaneous initiation of five carpel primordia (C, only two labeled) in positions alternate and interior to the inner stamen primordia. No carpel ring meristem is present. 5.13. Oblique polar view of androecium and gynoecium on a common elevated platform. The inner stamen primordia are in an early stage of differentiation; this is apparent by elongated bases and broadened two-lobed apices. Five carpel primordia are present.
Figs. 5.14 - 5.19. *Sterculia ceramica*, proliferation and development of the androecium and development of the gynoecium. Bars = 200 µm. 5.14. Androecial primordia and star-shaped young gynoecium. The carpels radiate outward rather than upward, and each has a radial groove. 5.15. Oblique lateral view of the androecium. The inner androecial whorl now occupies a terminal position on a short androecial tube and has five two-lobed stamen primordia. The outer whorl of the androecium has developed into five meristematic pads positioned on the sides of the androecial tube. Each of these staminal meristematic pad has many primordial mounds. 5.16. Lateral view of young androecial tube. The five inner stamen primordia are at the top of the tube. The shape of the outer staminal meristematic pads and the number and position of staminal mounds on each varies within this flower and others. In general, each meristematic pad appears to have between six and nine staminal mounds. 5.17. Polar view of gynoecium and partially dissected androecium. The inner stamen whorl has been removed. The carpels are oriented vertically to obliquely vertical. Each carpel has an adaxial crevice. 5.18. Lateral view of androecium. The anthers are sessile. The upper (outer) stamens have tetrasporangiate anthers and the lower ones are in various stages of anther differentiation. Some of the young carpel tips protrude among the anthers on the side of the androecial column. 5.19. Partially dissected androecial column to reveal five carpel tips. All the anthers are tetrasporangiate and sessile on the column.
Figs. 5.20 - 5.25. *Sterculia ceramica*, mid and late stage floral development. Bars = 250 μm in 5.20 and 5.21, = 2 mm in 5.22 - 5.24, = 20 μm in 5.25. 5.20. Longitudinal dissection of a floral bud. The immature calyx is thick and forms a protective dome over the inner floral organs. The elevated gynoecium is surrounded by and attached basally to the androecial tube (Ad). 5.21. Partially dissected gynoecium revealing a locule in each carpel and two ovules (O, only one labeled) in one of the locules. 5.22. Flower bud with part of the calyx removed. Glandular trichomes have developed on the upper inner surface of the sepals. The androecium consists of numerous tightly crowded sessile anthers. 5.23. Androecial column and gynoecium. The anthers, that occupy the upper portion of the elongated androecial column, have been removed. The carpels are positioned on a raised central portion of an androgynophore (where they would be surrounded or surpassed by the anthers). The calyx is very thick relative to the rest of the floral organs. 5.24. Longitudinal dissection of a floral bud at anther dehiscence. This flower has four sepals (two removed) which are fused most of their length into a tube. The upper portion of each sepal, beyond the point of connation, flares outwardly. The androecium is included and the anthers have dehisced by longitudinal slits. The gynoecial members are not exserted beyond the androecium. 5.25. Pollen grains are spheroidal and tricolporate and have raised reticulate surface texture.
It is not uncommon to have various sizes of follicles or to have some aborted follicles in a fruit. Each follicle typically contains two or three small, smooth, brown seeds.

**Herrania sp. (Sterculiaceae)** -- **Organography** -- The plant is a small monopodial tree or treelet of forest understory. The maroon flowers are in small to large cauliflorous clusters. The calyx appears to be three- to five-merous. The corolla is five-merous with long petal appendages. The androecium includes fertile stamens as well as petaloid sterile stamens. The gynoecium forms a syncarpous ovary.

**Initiation and early development of the calyx** -- Each flower is subtended by three helically initiated floral bracts that vary in size and slightly in vertical position on the pedicel (Fig. 5.26). Sepal primordia initiate in helical sequence, without a ring meristem (Fig. 5.26). Critical stages are not available to determine if total sepal number is three, or if more initiate. In the next stages available, the sepals form a very pubescent connate dome over the internal floral organs.

**Initiation and early development of the corolla and androecium** -- The floral apex to the interior of the calyx becomes pentagonal in outline. Then the apex develops a shallow central depression concurrently with the initiation of five common mounds (common petal/first-whorl stamen mounds) along the raised periphery. The common petal/first-whorl stamen mounds initiate simultaneously in the corners of the five-angled apex (Fig. 5.27). As these mounds become larger and expand outwardly, five smaller stamen primordia (the second whorl members) initiate simultaneously in positions alternating with the five common petal/first-whorl stamen mounds (Fig. 5.28). Then, a very low petal-stamen ring meristem becomes more defined (Figs.
5.28, 5.29). Each of the common mounds subdivides (partitions) into an outer petal primordium and two side-by-side first whorl (sometimes common) stamen primordia in the petal radius (Fig. 5.29). In this case, designation of first stamen whorl begins with the initiation of the common petal/first-whorl stamen primordia, even though the discrete stamen primordia develop later. Since at these early stages of initiation the first and second whorls of stamen primordia appear in the same spatial whorl (i.e. both are equidistant from the central axis), I prefer not the use the terms inner and outer whorls until later in development. Generally, one member of each associated pair of first-whorl (common) stamen primordia is larger and broader radially than the other (Figs. 5.29 - 5.31). Some or all of these larger first-whorl (common) stamen primordia become two-lobed (Figs. 5.30, 5.31), then somewhat peanut-shaped (Fig. 5.32), and ultimately bifurcate radially into two stamen primordia each (Figs. 5.33 - 5.35). Thus the first whorl includes 10 to 15 stamens. The second whorl initiates as discrete stamen primordia that do not subdivide and therefore, includes only five members. Each stamen primordium in the first whorl develops a short stalk (filament) and becomes distally broad and two-lobed (Figs. 5.33, 5.34). The stamen primordia in the second whorl do not broaden apically, but rather elongate into short, incurved finger-like structures (Figs. 5.33, 5.34). As this is occurring, the first stamen whorl assumes a position outside the second stamen whorl; thus, the term outer whorl now applies to the first whorl and inner whorl now applies to the second whorl. With further differentiation of the outer stamens, two pollen sacs develop in each of the deeply defined anther lobes (Fig. 5.35). The process of differentiation lags behind in the more centrifugal members of the outer stamen whorl (Figs. 5.33 - 5.35). Members of the inner stamen whorl
become laminar and lack any external evidence of pollen sacs (Fig. 5.35). Meanwhile, the petals become laminar (Figs. 5.32 - 5.35), and the petals and the fertile stamen filaments remain short (i.e. elongation is retarded).

**Initiation and early development of the gynoecium** -- The pre-carpel apex is initially flat and circular to almost pentagonal in outline (Fig. 5.29). At about the time that some of the first whorl of common stamen primordia are becoming two-lobed, five carpel primordia initiate simultaneously without a ring meristem (Fig. 5.31). The carpel primordia are positioned on the petal radii (Figs. 5.31 - 5.35). Each carpel primordium develops an adaxial dimple (Fig. 5.32), then a crevice (Figs. 5.33, 5.34), and ultimately a locular crevice (Figs. 5.35 - 5.37). A syncarpous ovary with five small apical lobes forms (Figs. 5.35 - 5.37). In each locule, two vertical rows of ovules initiate; each row is positioned posteriorly on a carpel side wall (Figs. 5.36, 5.37). Initiation and development of the ovules progresses acropetally (Figs. 5.36, 5.37). Only a minute apical residuum persists in the center of the young gynoecium (Fig. 5.36).

**Midstage and late floral development** -- Young buds are more or less globose (Fig. 5.38). The pedicels do not appear to be jointed. Prior to anthesis, the calyx members fuse into a thick, pubescent dome (Fig. 5.38). A trichomatous nectary develops on the inner base of the calyx (Figs. 5.39, 5.41). The corolla and androecium do not elongate until after the gynoecium has developed a syncarpous ovary (Figs. 5.38, 5.39). Each petal develops a long incurled apical appendage; and the rest of the petal becomes shallowly cup-shaped with inflexed lateral margins (i.e. similar in shape to the blade of a coal shovel) (Fig. 5.41). The petals are adnate basally to the outer stamen groups (Fig. 5.34). The outer stamens are fertile with tetrasporangiate
Figs. 5.26 - 5.31. *Herrania sp.*, initiation of the calyx, corolla, and androecium. Bars = 100 μm. 5.26. Helical initiation of some sepal primordia (sequence of initiation shown with numbers). Three floral bracts of various size subtend the flower. 5.27. Floral apex to the interior of the connate calyx (sepals have been removed). The center of the apex is depressed and five common petal/first-whorl stamen mounds (m, only one labeled) have initiated simultaneously on the upper periphery. 5.28. Initiation of the five members of the second whorl of stamens (sSt) in the same spacial whorl but alternate with the larger common petal/first-whorl stamen mounds. 5.29. Partitioning of each common mound into an outer petal primordium (P) and two side-by-side stamen (common) primordia (members of the first stamen whorl, fSt). The remaining floral apex is relatively flat and circular to somewhat pentagonal in outline. 5.30. Polar view of floral structures. The petals and (common) stamen primordia have become more defined. Some of the first stamen whorl members are two-lobed (*). 5.31. Oblique view of flower bud in Fig. 5.30. Five carpel primordia (only one labeled) are present.
Figs. 5.32 - 5.37. *Herrania* sp., early development of corolla, androecium, and gynoecium. Bars = 200 μm. 5.32. Young gynoecium with an adaxial dimple in each carpel. The petals radiate more upward. Some of the first whorl of stamen primordia are peanut-shaped (*). 5.33. The first whorl of stamen primordia have assumed positions outside the second whorl of stamen primordia; therefore, the designations of outer and inner stamens whorls (respectively) apply. Most of the outer whorl of stamen primordia are apically two-lobed; a more centrifugal member lags behind in differentiation (*). The members of the inner stamen whorl are terete and arch inwardly. The carpel primordia are fused basally and have adaxial crevices. The petals have become more laminar. 5.34. Oblique view of a young, partially dissected flower. The outer stamen primordia have very short stalks (filaments, some at arrows) and are two-lobed apically. Some peripheral outer stamen primordia are present and lag behind in development (*). The carpels have locular crevices. 5.35. Partially dissected androecium and corolla. Each stamen primordium in the outer whorl has four pollen sacs, two per anther lobe. The inner stamen primordia are laminar and arch inwardly. The petal tips are curled slightly inward. The gynoecium has elongated vertically into a dome with five apical lobes. 5.36. Longitudinally dissected gynoecium. Very little apical residuum (r) remains interior to the gynoecium. Ridges (at arrows) on the side walls of the locules indicate the initiation of ovules. 5.37. Partially dissected syncarpous ovary revealing vertical rows of acropetally initiated ovule primordia (O, only two labeled).
Figs. 5.38 - 5.41. *Herrania sp.*, midstage floral development. Bars = 1 mm in 5.38 and 5.41, = 250 μm in 5.39 and 5.40. 5.38. Partially dissected calyx revealing lateral view of internal floral organs. The calyx members are fused into a thick, very pubescent dome. 5.39. Oblique view of flower bud with calyx removed. Each petal has developed a small apical appendage. The tetrasporangiate anthers are more defined but the filaments have not elongated significantly. A trichomatous nectary (N) has developed on the inner surface of the sepal bases. 5.40. Young syncarpous ovary (V) with ten vertical bulges or ribs. A short stylar column (sl) with five apical lobes has developed. 5.41. Immature flower with sepals and one petal removed. The outer stamens are in five antepetalous groups with two or three members in each group. Anthers are tetrasporangiate. Each petal has a long incurled apical appendage, and the lower portion is shallowly cup-shaped with incurved lateral margins. The apical portion of each petaloid inner stamen bends in a centrifugal direction. The sepal trichomatous nectary is visible.
anthers and are arranged in five antepetalous groups with two or three members in each group (Figs. 5.39, 5.41). The five inner sterile staminodes are petaloid and are reflexed outward (Fig. 5.41). The ovary becomes vertically ten ribbed and develops a short stylar column with five apical lobes (Fig. 5.40).

The late stage buds and mature flowers in my collection are in too poor a condition to make reliable observations about their morphology, so I will summarize what little is available from the literature. At maturity, the petals are hood-like (Baillon, 1875; Cuatrecasas, 1964) with remarkably long linear appendages that are pendulous at anthesis (Cuatrecasas, 1964; Gentry, 1993). The staminal filaments are "asymmetrically parted in two branches, one 1-antheriferous, the other 2-antheriferous" and are depicted as attached to a short androecial tube in an alternating pattern with the staminodes (Cuatrecasas, 1964). This is explainable if the outer stamens that resulted from a bifurcation event share a common base (i.e. partially or completely fused filaments) and the adjacent stamens, which did not bifurcate, have distinct filaments; and then the androecium was elongated basally to form a short tube. Pollen grains are characterized as prolate (elongate in the direction of the poles) (Cuatrecasas, 1964) and the fruits are large, oblong, vertically ribbed, berrylike, and supposedly edible (Gentry, 1993).

**Pachira aquatica** (*Bombacaceae*)  --  Organography  --  The plants are evergreen trees, usually with buttresses. The flowers are very large, showy, bisexual, and mostly solitary or sometimes in groups of two or three. The three-merous involucel is caducous and the receptacle is five-glandular. The calyx is five-merous and the sepals are connate. These outer
perianth parts, the receptacle, and sometimes the pedicel are covered with minute yellowish-brown hairs. The five petals are long, narrow, and usually whitish (or greenish or yellowish). The basally monadelphous androecium is comprised of numerous stamens (apparently in two whorls) with extremely elongate filaments and bisporangiate anthers. The gynoecium has a syncarpous five-locular ovary, fused stylar column, and a five-parted stigma, and produces a large capsule.

**Initiation and early development of the outer perianth** -- Floral apices are more nearly circular in outline and more elevated (Fig. 5.43) than vegetative apices (Fig. 5.42). The first bractlet primordium is broad laterally as is a leaf-stipule primordium, but the second and third bractlet primordia are more nearly circular in outline (Figs. 5.43, 5.44). The bractlet primordia initiate helically on the periphery of the floral apex and no ring meristem is present (Figs. 5.43, 5.44). With further development, bractlets are typically inserted at different vertical levels at the base of the flower bud, with at least one generally lower than the other two (Figs. 5.47, 5.50). In addition, the bractlets may differ slightly in size. Sepal primordia appear to initiate in a helical sequence (Figs. 5.45 - 5.47). It is not known if a ring meristem precedes sepal initiation, but very early in development the primordia are fused basally. The calyx and the inner floral apex are elevated above the bractlets on a broad base (Figs. 5.46, 5.47). The connate sepals elongate to form a protective dome over the remaining inner floral organs (Fig. 5.60).

**Initiation and early development of the corolla and androecium** -- The pre-petal floral apex is pentagonal in outline and relatively flat (Figs. 5.45, 5.46). Next, five common mounds initiate simultaneously along the periphery and a central depression develops on the apex (Fig. 5.48). Each of the
common mounds subdivides (partitions) into a peripheral petal primordium and two side-by-side common outer-stamen mounds that are in the petal radius (Figs. 5.49, 5.50). As this is occurring, a petal-stamen ring meristem becomes more pronounced (Figs. 5.49, 5.50). Next, five common inner-stamen primordia initiate simultaneously in positions interior and alternate to the petal/outer-stamen groups (Fig. 5.51). As the petals enlarge, they become laminar and arch over the androecium (Fig. 5.51). With continued enlargement of the petal-stamen ring meristem, the ten common outer-stamen mounds become meristematic pads which get broader and taller centrifugally (Figs. 5.52 - 5.55). Each of these outer meristematic pads partitions radially (Fig. 5.52) and then in a combination of radial, lateral, and oblique directions until many common stamen primordia form on each pad (Figs. 5.53 - 5.55, 5.58). The common stamen primordia that develop on each pad are of various sizes (Figs. 5.54, 5.55). Members of the inner whorl of common stamen mounds also divide at least once; it is unclear if this process is partitioning or bifurcation (Figs. 5.54, 5.55, 5.58). Each of the common stamen primordia then develops a short stalk and becomes apically broad and two-lobed (Figs. 5.59, 5.61, 5.62). Subsequent bifurcation of these common primordia typically results in paired stamens with basally fused filaments.

**Initiation and early development of the gynoecium** — The five carpel primordia initiate simultaneously in the petal radii (Figs. 5.52, 5.56). The carpels initiate at about the time of the first partitioning events of the outer common stamen mounds and prior to partitioning of the inner stamen mounds (Figs. 5.52, 5.53, 5.56). Soon after initiation, the carpel primordia become confluent to form a connate base (Fig. 5.58). During early
Figs. 5.42 - 5.47. *Pachira aquatica*, vegetative shoot and floral buds with initiation of the involucel and early development of the calyx. Bars = 200 μm. 5.42. Polar view of vegetative shoot. Some leaves (L) and stipules (sp) have been removed. 5.43. Floral apex that is surrounded by primordia of leaves with paired stipules. The larger of the floral apices has two bractlet primordia (Bt). 5.44. Helical initiation of three bractlet primordia on the periphery of a floral apex (sequence of initiation is shown with numbers). 5.45. Five helically initiated sepal primordia (sequence of initiation shown with numbers). 5.46. Lateral view of the flower bud in Fig. 5.45. The calyx and the remaining apex are on a broad elongated base. The floral apex is pentagonal in outline and relatively flat except for slight mounding in the corners. 5.47. Oblique view of flower bud. The bractlet scars are at different vertical levels around the bud. The sepals are arched over the inner portion of the flower (sequence of initiation is shown with numbers). The floral apex has a central depression.
Figs. 5.48 - 5.53. *Pachira aquatica*, initiation of petals, stamens, and carpels. Bars = 200 μm. 5.48. Five common petal-outer stamen mounds (only one labeled) have initiated simultaneously. A shallow depression has developed in the center of the apex. 5.49. Petal-stamen ring meristem. Each common mound has partitioned into a peripheral petal primordium and two side-by-side common outer stamen mounds that are in the petal radius. 5.50. Polar view of bud with bractlets and sepals removed. Five petal primordia and ten common outer stamen mounds are present. The outer portion of the petal-outer stamen ring has elongated. 5.51. Petal primordia are laminar and arch inwardly over the androecium. Five common inner stamen primordia have initiated interior and alternate to the petal-outer stamen groups. The order of initiation within the inner stamen whorl is simultaneous. 5.52. Petal-stamen ring meristem. The petals have been removed. Each of the original ten common outer stamen mounds (now meristematic pads) has partitioned radially into two or three common stamen primordia. The common inner stamen primordia have elongated centripetally. Five carpel primordia are present. 5.53. Further enlargement and partitioning (this time in radial and lateral directions) of the outer stamen meristematic pads. Each carpel primordium has an adaxial dimple.
Figs. 5.54 - 5.59. *Pachira aquatica*, stamen proliferation and carpel initiation. Bars = 250 \( \mu \)m in 5.54, 5.55, 5.58, and 5.59, = 100 \( \mu \)m in 5.56 and 5.57. 5.54. Polar view of androecium with ten outer stamen meristematic pads. Each meristematic pad has many common stamen primordia. Each common inner stamen primordium is two-lobed apically. The gynoecium has five carpel primordia, each with an adaxial crevice. Carpels are in the petal radii. 5.55. Oblique view of an androecium at a slightly more advanced stage of partitioning. 5.56. Gynoecium and partially dissected androecium. Five carpel primordia have initiated simultaneously in the petal radii. 5.57. Five carpel primordia. A small apical residuum remains to the interior of the gynoecium. 5.58. Basally-fused carpel primordia and partially dissected androecium. 5.59. Common outer stamen primordia with elongated bases and two-lobed apices. Additional partitioning events have occurred in the inner stamen whorl. Stigmatic surfaces have started to develop on the carpel tips.
Figs. 5.60 - 5.65. *Pachira aquatica*, midstage floral development. Bars = 1 mm, except in 5.61 and 5.65 = 500 μm. 5.60. Small flower bud. The calyx is connate and has five glands at the base (G, only one labeled). The three bractlets have been removed. 5.61. Lateral view of androecium and gynoecium. Some petals have been removed. Each of the common outer stamen primordia are two-lobed. 5.62. Contort petals inside of a thick calyx. Some of the common outer stamen primordia have elongated bases. 5.63. Immature androecium and gynoecium. The outer stamen primordia are in ten fascicles (five antepetalous pairs of fascicles) with many members in each. The stamens are of various sizes. The filaments are usually fused basally into pairs (at arrows). Anthers are bisporangiate. 5.64. Different view of Fig. 5.63. The styles are fused into a column with a five-parted stigma. The ovary is relatively flat and on about the same plane at the androecial members. 5.65. Immature stigma.
developmental stages, a small apical residuum remains interior to the gynoecium (Figs. 5.57, 5.58). Each carpel develops an adaxial dimple (Figs. 5.53, 5.57), then an invagination (Fig. 5.58), and then a locular crevice (Fig. 5.59). Two vertical rows of ovules initiate in each locule. The apical portion of each carpel develops a rough stigmatic surface even before the stylar column has elongated significantly (Figs. 5.59, 5.61).

Mid and late stage development -- The nonjointed pedicels are very thick. The bractlets remain relatively small and fall off before the bud reaches maturity. The calyx dome becomes thick, tough, and for the most part covered with short trichomes (Figs. 5.60, 5.62). Five glandular areas develop along the outer base of the calyx in the area of the receptacle (Fig. 5.60) and become more defined with bud enlargement. At anthesis, the sepals fuse into a short tube (much shorter than the corolla) that may be apically smooth, undulate, or one- to five-lobed. In the bud, the petals form a contorted corolla and are adnate to the androecial base (Figs. 5.61 - 5.64). At maturity, the petals are long and linear, and have tufted hairs on the lateral claw margins. The corolla generally slightly exceeds the fertile floral organs in height. The androecium has an outer whorl with ten fascicles (clusters of stamens) and an inner whorl with five fascicles (Figs. 5.63, 5.64). The stamens vary in height and usually the filaments are fused basally in pairs (Figs. 5.63, 5.64). Each stamen produces a bisporangiate anther (Figs. 5.63, 5.64). At maturity, the androecium elongates into a column with numerous long filaments diverging from the summit. The gynoecium forms a single stylar column with five pointed stigma lobes (Figs. 5.64, 5.65). At maturity, the gynoecium is about the same height or slightly taller than the stamens. The capsule is
subglobose, ellipsoid, or oblong-ellipsoid with five longitudinal grooves; and the pollen is tricolp(orate)ate (Robyns, 1964).

**DISCUSSION**

**The involucel** -- Although most members of the Bombacaceae and Sterculiaceae have an involucel, only one of the three outgroup taxa examined in this paper (*Pachira aquatica*) has an involucel (involucellar bracts or bractlets). In *P. aquatica* the three bractlets initiate on the floral apex in helical sequence without a ring meristem. These bractlets remain unfused, are positioned at various levels on the pedicel, and are caducous. Although Rao (1952), van Heel (1966), and Moncur (1988) examined some taxa in these two families that have involucels, they did not describe bractlet initiation.

**The calyx** -- Merosity of the calyx varies among the taxa, with five in *Pachira aquatica*, four (less often three or five) in *Sterculia ceramica*, and three (or more?) in *Herrania sp.* In all these species, the calyx functions in early protection of the inner floral organs. In *S. ceramica*, which lacks petals, the cream-colored sepals may also function as attraction for pollinators in mature flowers. In *P. aquatica*, the overall color of the calyx is brownish rather than green; however, the long brush-shaped androecium clearly dominates other organs in appearance. In all of these taxa, the sepals are connate to some extent. Trichomatous nectaries are present on the inner sepal bases in *Herrania sp.* and *P. aquatica* and on the inner sepal apical lobes in *S. ceramica*. Although these three taxa vary in sepal number, taxa of Bombacaceae and Sterculiaceae typically have five-merous calices (van Heel, 1966). In addition, most taxa in these two families are reported to have connate sepals and sepal nectaries (van Heel, 1966).
The order of sepal initiation is helical in all three taxa. A sepal ring meristem is lacking in *Sterculia ceramica* and *Herrania sp.*; this stage of development was unavailable in *Pachira aquatica*. Similarly, helical sepal initiation and an absence of a sepal ring meristem are reported in *Theobroma cacao* (Sterculiaceae) (Bayer and Hoppe, 1990). Rao (1952), van Heel (1966), and Moncur (1988) did not discuss sepal initiation in their descriptions of members of these two families.

**The corolla** — The corollas are five-merous in *Herrania sp.* and *Pachira aquatica*, and are lacking in *Sterculia ceramica*. In *Herrania* and *P. aquatica* the petals lack connation, are adnate to the base of the androecium, exceed the sepals in length, and at maturity flare to form an open flower, i.e. nontubular. The color of the corolla varies, from maroon in *Herrania sp.* to whitish in *P. aquatica*. The petals in *Herrania sp.* form hoods with long linear apical appendages. In *P. aquatica* a pair of ciliate tufts occurs on each petal claw.

Bombacaceous corollas are typically five-merous, lack connation, and in most taxa they are adnate to the androecium (van Heel, 1966). The petals adhere to the staminal tube in *Bombax ceiba* (Bombacaceae) (Davis and Mariamma, 1965). In the Sterculiaceae, the petals are five-merous and unfused or are absent (van Heel, 1966). When present, the petals are usually not adnate to other organs, although a few exceptions are found with adnation to the androecium and sometimes additionally to the calyx (van Heel, 1966). Contrary to my findings, van Heel (1966) listed *Herrania albiflora* without petal adnation; it is possible this is a species difference or a character that was overlooked.
The early ontogeny of the corollas in *Herrania* sp. and *Pachira aquatica* are similar. In both there is a clear association between the corolla and the androecium. The petal primordia result from partitioning of common petal/first-whorl stamen mounds. A low petal-stamen ring meristem forms concurrently with or after the formation of the five common petal/first-whorl stamen mounds. The order of petal initiation is simultaneous. The petals are positioned exterior to and on the same radii as members of the first stamen whorl and alternate to members of the second stamen whorl. In *Herrania* sp., petals do not elongate until after the anthers have started to differentiate, whereas in *P. aquatica* the petals elongate significantly during the proliferation of the androecium and are relatively tall at the onset of anther differentiation. In *Sterculia ceramica*, there is no externally visible evidence of petal initiation.

Close association between the corolla and androecium may not be a consistent feature in all Sterculiaceae and Bombacaceae. In *Theobroma cacao* (Sterculiaceae) the petal primordia initiate independently of the androecium on a convex apex, i.e. no common petal-stamen mounds or a petal-stamen ring meristem (Bayer and Hoppe, 1990). The petals in *Thomasia pauciflora* (Sterculiaceae) are characterized as probably originating independently and then being later suppressed so that the mature flowers (that have adnate perianth-stamen cups) lack petals (van Heel, 1966). Common petal-stamen mounds initiate in *Durio zibethinus* (Bombacaceae) (based on figures in Moncur, 1988) and *Bombax ceiba* (Bombacaceae) (Davis and Mariamma, 1965; van Heel, 1966). A common petal-stamen ring meristem has been alluded to in *Quararibea guianensis* and *Ochroma lagopus* (Bombacaceae) (van Heel, 1966) and in *Matisia*
cordata (Bombacaceae) (based on figures in Moncur, 1988). Petal initiation has been described in relatively few taxa in these families and most of the previous literature is unclear about the association between the corolla and the androecium. Obviously, many more taxa need to be examined to discover how the petals originate and to determine the prevalence of common petal-stamen primordia and petal-stamen ring meristems in Sterculiaceae and Bombacaceae.

Androecium — Several mature androecial features vary among the taxa. Stamen numbers vary from 15 to 20 in Herrania sp. to more than 30 in Sterculia ceramic and more than 150 in Pachira aquatica. In P. aquatica the stamens are long exserted beyond the calyx and are only slightly shorter than the narrow petals, whereas in S. ceramic they are included in the calyx; this character was not determined for Herrania sp. The stamen filaments in P. aquatica depart apically from the androecial tube, whereas in the other taxa the filaments (sessile anthers in the case of S. ceramic) depart from the upper levels of the tubes.Filaments diverge from the androecial column both singly and in pairs in Herrania sp. and mostly in pairs in P. aquatica. Herrania sp. contains both fertile stamens and sterile petaloid stamens. S. ceramic has two types of fertile stamens; the inner stamens appear to produce larger and broader-based anthers which are oriented in a different direction from the outer stamens. Anthers in S. ceramic and Herrania sp. are tetrasporangiate, whereas in P. aquatica they are bisporangiate. Anthers dehisce by longitudinal slits in S. ceramic and P. aquatica; this character was not determined for Herrania sp.

The stamen numbers found in these three taxa are not unusual for the families; stamen numbers in both Bombacaceae and Sterculiaceae may
range from five to numerous (van Heel, 1966). It appears, however, that most Sterculiaceae are at the low end of the stamen merosity range, whereas the Bombacaceae have mostly higher stamen numbers (van Heel, 1966). Staminodes, such as those in *Herrania*, are typical of many Sterculiaceae according to Benson (1957), Cronquist (1981), van Heel (1966), and Heywood (1985). Although *Pachira* and most other bombacaceous taxa do not have staminodes or petaloid stamens, they have been reported in *Durio acutifolius* (van Heel, 1966). Heterostemony has also been reported in *Bombax ceiba* (Bombacaceae) (Davis and Mariamma, 1965). The number of sporangia per anther is a familial characteristic, with Bombacaceae having bisporangiate anthers and Sterculiaceae having tetrasporangiate anthers (Cronquist, 1981; Gentry, 1993).

The androecia of *Sterculia ceramica*, *Herrania sp.*, and *Pachira aquatica* share several developmental characteristics. At least some basal fusion occurs in the androecium so that a tube or column forms. Sterile androecial teeth are lacking in these taxa at maturity and there is no external evidence of initiation of these structures. Partitioning events occur in all the androecia, at least in the first (outer) whorl of stamens. Hence, some stamen primordia result from division of common meristematic regions, pads, or mounds. Typically, the stamen primordia are not arranged in radial rows. Lastly, all three taxa examined in this research have two whorls of stamens, though this may only be evident by examining early ontogeny.

Most members of the Sterculiaceae and Bombacaceae develop an androecial tube (van Heel, 1966). This feature is not fully developed until late stages of floral development in Sterculiaceae according to van Heel (1966). Sterile androecial teeth or extensions of the sterile androecial tube

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are not typical of members in these two families, but they have been reported in several members of the Bombacaceae (Bombax, Matisia, Quararibea, and Ochroma) (van Heel, 1966). The stamen primordia in most Sterculiaceae and in many Bombacaceae have been described as arranged in a "wave-line" (somewhat radial rows) on the androecial tube, in a manner that is similar to the Malvaceae (van Heel, 1966). Exceptions to this in Bombacaceae include: Adansonia digitata with stamen primordia that cover the entire androecial tube, Pachira spp. and Durio spp. with the stamens arranged in groups or fascicles, and Ceiba spp. with only a five-merous androecium (van Heel, 1966).

The androecium of Sterculiaceae typically has two whorls of organs according to most previous researchers. Two exceptions are Ruizia which may have three whorls more or less and Eriolaena which may have one to three whorls (van Heel, 1966). The outer whorl of stamens is commonly reduced to staminodes or suppressed and the inner whorl bears normal anthers according to Heywood (1985) and Gentry (1993); these authors did not specify which stamen whorl is antepetalous and which is antesepalous. In contrast, van Heel (1966) and Cronquist (1981) described the outer or antepetalous stamens or groups of stamens as normal and the inner or antesepalous stamens as commonly staminodial, petaloid, or suppressed (sometimes normal). My research with Herrania sp. supports the latter, with the outer antepetalous first-stamen whorl having fertile stamens and the inner alternipetalous second-stamen whorl being sterile (petaloid). A comparable arrangement of fertile and sterile stamens was depicted in Theobroma cacao (Baillon, 1875; Moncur, 1988; Bayer and Hoppe, 1990). Similar to my findings in Sterculia ceramica, van Heel (1966) reported that several species

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of *Sterculia* have two whorls of fertile stamens; but he also described some species that lack the inner whorl.

Little information is available in the literature about the number of stamen whorls in members of the Bombacaceae. Only one androecial whorl may initiate in *Ceiba, Chorisia* and *Camptostemon* pro parte (van Heel, 1966), and *Durio zibethinus* (based on figures in Moncur, 1988). Some taxa reportedly have two stamen whorls (*Adansonia, Pachira, Bombax,* and some *Camptostemon*) and some have three (*Durio* and *Quararibea*) (van Heel, 1966). In *Matisia cordata* "whorls of stamens" are described by Moncur (1988), but his micrographs seem to indicate one whorl with many sets. In the bombacaceous taxon that I examined, *Pachira aquatica*, there are two stamen whorls in the androecium. One source of confusion in previous literature (e.g., van Heel, 1966; Moncur, 1988) is that, what I refer to as sets within a whorl, they may refer to as multiple whorls. For the most part, however, the early stages of androecial development that would determine how many whorls initiate have not been observed by previous researchers.

There are several major differences in early ontogeny of the androecia among the taxa I examined. First, in *Sterculia ceramica* the early (common) androecial primordia initiate on a slightly convex floral apex; there is no androecial ring meristem. Both *Herrania sp.* and *Pachira aquatica* initiate a low petal-stamen ring meristem. Second, common petal/first-whorl stamen mounds are present in *Herrania sp.* and *P. aquatica*, but not in *S. ceramica*. Third, in *S. ceramica* the two stamen whorls initiate at the same time, with one whorl exterior to the other. In *P. aquatica*, the outer stamen whorl initiates prior to the inner stamen whorl. In *Herrania sp.* the two stamen whorls initiate consecutively, but in the same spacial whorl and only later in
development does the second whorl take a more interior position to the first. Also, the inner (second) stamen whorl initiates sooner in *Herrania* sp. than in *P. aquatica*, i.e. during, as opposed to after, partitioning of the common petal/first-whorl stamen mounds into petals and common stamen mounds.

Fourth, *Herrania* sp. does not form androecial meristematic pads, but *S. ceramica* and *P. aquatica* form multistamen meristematic pads in the first (or outer) stamen whorls. In addition, the orientation of these meristematic pads differs between the taxa; in *S. ceramica* the meristematic pads are abaxial and vertical on the developing androecial tube, whereas in *P. aquatica* the pads are adaxial and sloped inward. A fifth difference is that during the early stages of stamen proliferation, *S. ceramica* has pronounced elongation of the androecial tube. In the other two taxa the androecial tube does not significantly elongate until after the individual stamen primordia have started to differentiate. A sixth character difference is that *S. ceramica* develops an androgynophore, a unique feature among the three taxa. Lastly, although bifurcation of some common stamen primordia occurs in *Herrania* sp. and *P. aquatica*, bifurcation events are not evident in *S. ceramica*.

The presence of common stamen mounds and androecial ring meristems are not consistent features among the Sterculiaceae. Van Heel (1966) generalized that the androecial wall (i.e. ring meristem) may be extremely low or absent; though it should be noted that he observed early androecial development in only a few sterculiaceous taxa. In addition, he stated that “the existence of staminal lobes” (common mounds) “as parts of a pentagonal wall” (ring meristem) “has not been demonstrated, except in *Fremontia californica*”. In *F. californica*, he portrayed the androecium as initiating as five mounds which subsequently fuse laterally. It should be
noted that although *Fremontia* has conventionally been placed in the Sterculiaceae, there is mounting evidence that it belongs elsewhere (Fryxell, personal communication 1999). Van Heel's (1966) characterization of *Sterculia* spp. differs from my findings with *Sterculia ceramica* in that he described an androecial wall (ring meristem), whereas I found no androecial ring meristem. *S. ceramica*, however, was not one of the many species he examined.

Although *Herrania sp.* is a segregate of *Theobroma*, there are several notable differences in early initiation of the androecium. In one depiction of *Theobroma* spp. the petals initiate in the corners of a "flat five-angled receptacle" and interior to this "a five-angled ring of stamen primordia" develops; this stamen ring meristem bears both the antesepalous and antepetalous primordia (van Heel, 1966). In another scenario, the androecium of *Theobroma cacao* initiates separately from the corolla on a convex apex, i.e. no common petal-stamen primordia or ring meristem are present (Bayer and Hoppe, 1990). This differs from my characterization of *Herrania sp.* with common petal/first-whorl stamen mounds and a petal-stamen ring meristem. The early ontogeny of the androecium of *Herrania* was not described by van Heel (1966). Later stages of *Theobroma* androecial development that are described by Bayer and Hoppe (1990) are similar to my observations in *Herrania sp.;* the outer common stamen primordia divide (partition) and develop normal anthers and the inner stamen primordia develop into staminodia.

Most of the bombacaceous taxa are characterized by a "wall" (i.e. ring meristem) on which the androecial members initiate; though in some taxa the very early stages of the androecia have not been observed (van Heel, 1966).
A petal-stamen ring meristem has been alluded to in *Quararibea guianensis* and *Ochroma lagopus* (van Heel, 1966) and in *Matisia cordata* (based on figures in Moncur, 1988). Common petal-stamen mounds have been described in *Bombax ceiba* (van Heel, 1966). According to van Heel (1966), common stamen "buttresses" (mounds and pads) are not uncommon in Bombacaceae, especially in the outer stamen whorls. *Durio zibethinus* initiates common petal-stamen mounds and then develops five meristematic stamen arches (based on figures in Moncur, 1988). Van Heel's (1966) description of the ontogeny of the androecium in *Pachira spp.* resembles mine except that he did not observe the early stages that have common petal-stamen mounds. Clearly, since the literature mostly lacks descriptions of early androecial development, and since discrepancies occur in what little is available, a closer look at the early ontogeny of the androecium is needed for more members of these two families.

**Gynoecium** – In the three taxa I examined, carpel number is five. In *Sterculia ceramica* the carpels do not fuse, whereas in *Herrania sp.* and *Pachira aquatica* the carpels fuse to form syncarpous ovaries. In *P. aquatica* the styles fuse to the level of the stigma lobes. Ovule number varies from two or three per locule in *S. ceramica* to many per locule in *Herrania sp.* and *P. aquatica*. The ovary is superior and placentation is marginal in *S. ceramica* and is axile in *P. aquatica* and *Herrania sp.* All of these characters are within the familial ranges reported earlier by previous researchers (Benson, 1957; Cronquist, 1968, 1981; Heywood, 1985; Gentry, 1993). Similar studies with SEM have depicted other members of the Bombacaceae, *Durio zibethinus* and *Matisia cordata* (Moncur, 1988) and *Theobroma cacao* (Bayer and Hoppe, 1990), with syncarpous gynoecia, fused styles, and five-lobed or
five-parted stigmas. In *Brachychiton australis* (Endress, Jenny, and Fallen, 1983; Jenny, 1983) and *Firmiana* (Jenny, 1983) (both Sterculiaceae) the apical portions of the carpels temporarily fuse postgenitally.

My collection of *Sterculia ceramica* is unusual in the apparent lack of a fully mature gynoecium even at anthesis. Although the carpels develop locular cavities with ovules, the carpels remain relatively small, are included within the androecial tube, and lack any obvious stigmatic structure. I also did not see any evidence of temporary postgenital apical or subapical fusion of the carpels at anthesis that has been described for *Sterculia* by Cronquist (1981) and Endress, Jenny, and Fallen (1983). According to Bailey (1935), in this genus the early flowers are unisexual or polygamous (staminate, pistillate, and hermaphroditic flowers at the same time) and the late or terminal flowers are commonly pistillate. The collection of *S. ceramica* that I obtained is from a large tree that had numerous young inflorescences as well as some mature inflorescences and mature fruits. All of the flowers I examined had both male and female organs, but I did not see fully mature gynoecia (i.e. with significant enlargement and development of stigmatic surfaces). Therefore, the nature of the gynoecium needs to be further investigated to determine the extent of development, timing of maturation, and the means of fertilization in this species.

In *Sterculia ceramica*, an androgynophore develops. This feature has been reported by van Heel (1966) in many Sterculiaceae (including *Sterculia*), but not in the Bombacaceae. According to van Heel (1966), the androgynophore develops late in ontogeny. Although this feature is more pronounced in late development, I found that (at least in *S. ceramica*) it
begins to develop during the early stages of stamen proliferation and at the onset of carpel initiation.

The three taxa share similar early ontogeny of the gynoecium, with the exception of fusion. No carpel ring meristem is present. In all, carpels initiate simultaneously, a small apical residuum is present interior to the young gynoecium, and all the carpels form locular cavities. In *Herrania* sp. and *Pachira aquatica* the carpels are positioned opposite to the petals. Carpel position in *Sterculia ceramica* is on the same radii as outer stamens; positions are complicated because it lacks petals and has a four-merous calyx whereas stamens and carpels are pentamerous. In *S. ceramica*, the very young carpel tips radiate outwardly, whereas in *Herrania* sp. and *P. aquatica* the very young carpel tips curve inwardly and upwardly.

A carpel ring meristem in *Durio zibethinus* (Bombacaceae) (Moncur, 1988) is one exception to the generally similar gynoecial development in the two families. The gynoecium in *D. zibethinus* is described as appearing as a mound of tissue with a hollow center and that subsequently it differentiates in five apical segments (Moncur, 1988). The gynoecium in *Theobroma cacao* (Bombacaceae) initiates as five indefinite bulges that subsequently fuse into a syncarpous ovary and later a fused stylar column (Bayer and Hoppe, 1990). Excepting the two aforementioned taxa, previous ontogenetic literature generally lacks descriptions of early gynoecial development in members of these two families.

**Fruit and pollen** – Three different fruit types occur among the representative taxa in this study. *Sterculia ceramica* produces a five-merous group of follicles. The fruits are described as vertically ribbed and berrylike in *Herrania* sp. (Gentry, 1993) and as capsules with longitudinal grooves in
*Pachira aquatica* (Robyns, 1964). All three fruits have overall dimensions that are taller than wide. The pollen in *Sterculia ceramica* is spheroidal, tricolporate, and rugose. Pollen in *Herrania sp.* is characterized as prolate (Cuatrecasas, 1964) and in *P. aquatica* as tricolporate (Robyns, 1964).

**Synopsis of floral distinctions in these three taxa** – The floral morphological characters that have in the past been used to describe these two families (outlined in the introduction) still apply, at least with respect to the three taxa I examined in this paper. The major morphological delineating feature has been sporangia number in the anthers; the two sterculiateous taxa have tetrasporangiate anthers whereas the bombacaceous taxon has bisporangiate anthers.

With so little ontogenetic information available in previous literature and with the limited number of taxa in this study, it is impossible to make broad generalizations about ontogeny in Bombacaceae and Sterculiaceae. The results obtained in this paper only relate to the specific taxa studied here. Since the familial affinities of the genera studied have generally not been in question, they can serve as representatives of their families and as outgroups for the cladistic analysis of Malvaceae.

These three taxa share several ontogenetic characteristics such as connation of the sepals, helical initiation of sepals, two whorls of stamens early in development, basal fusion of stamens into an androecial tube, and presence of some common stamen primordia or mounds. Based on ontogenetic data, however, *Sterculia ceramica* differs markedly from the other two taxa. Characters that distinguish *S. ceramica* include lack of a corolla, no petal-stamen ring meristem or androecial ring meristem, no common petal-stamen mounds, and presence of an androgynophore with an
apocarpous gynoecium and sessile anthers. Both *S. ceramica* and *P. aquatica* form multistamen meristematic pads in the first stamen whorl, but these differ in relative position (i.e. abaxial and vertical versus adaxial and sloped, respectively) on the developing androecial tube. *Herrania sp.* differs in having petals that form hoods with long appendages and in having a whorl of sterile petaloid stamens. When more taxa are examined in these two families, these differences may or may not be within the average range of diversity in each family. Therefore, the ontogeny of many more taxa in Sterculiaceae and Bombacaceae needs to be examined before any conclusions can be made about placement of certain taxa.

**Characteristics of Malvaceae** -- Previously, I examined floral initiation and development in 21 malvaceous taxa using SEM (Chs. 2, 3, 4). Generalizations about the Malvaceae are based primarily on results of this research and the literature described therein. For comparative purposes, a synopsis of malvaceous floral characteristics is provided.

Involucels are common in members of the Malvaceae. The number of bractlets may be three, four, five, or a variable number between four and fourteen (or more); or the involucel may be lacking. The bractlets initiate on the floral apex in helical sequence. A bractlet ring meristem may be present or absent depending on the species. In most taxa (with some exceptions), the bractlets are unfused, persistent, and positioned in a single spacial whorl directly below the calyx.

The calices in Malvaceae are five-merous and have trichomatous nectaries on the inner sepal bases. The sepals are connate to some extent. The sepals are valvate and function primarily as protection in the developing buds. In most taxa the calices are green. The species which have brightly-
colored calices (*Pavonia strictiflora* and *Malachra capitata*) also have corollas, but the main attractant in these flowers appears to be either the bractlets or the floral bracts. The sepals typically initiate in helical order. There are some exceptions with simultaneous initiation, all of which have helically initiated involucels that precede the calices. A sepal ring meristem is present in most taxa, though it is often poorly defined.

A five-merous corolla was always present, at least in the malvaceous taxa I examined. A wide range of colors (including white, cream, yellow, orange, pink, red, maroon, lavender, and even somewhat greenish) are present in the corollas. The corolla typically exceeds the calyx in height, but in a few cases doesn't exceed the involucel or floral bracts. The mature corolla usually flares to produce an open flower, but in a few taxa it forms a tubular flower. In the bud, the petals are convolute. Petal initiation typically overlaps with the early stages of initiation of the androecium. The petals initiate on a common petal-stamen ring meristem and often common petal-stamen mounds are involved. Initiation within the petal whorl is simultaneous. Petal elongation is generally delayed during proliferation of the androecium.

Stamen numbers vary from five to numerous in members of the Malvaceae. Usually the androecium is shorter than the corolla; the few exceptions to this are found in one tribe. In all the taxa, the stamens are fused basally into a column. Filaments may diverge singly, in pairs, or in groups from the column, rarely the anthers are sessile. The anthers are bisporangiate and dehisce by longitudinal slits. Sterile androecial teeth may be present or absent at the apex of the column. The androecium consists of only one stamen whorl (at least in the taxa I have examined), but it may
contain few to many sets of stamens that initiate in groups of five or multiples of five. Initiation within each stamen set is simultaneous. A petal-stamen ring meristem is a common feature in all the taxa I examined. There are, however, several ontogenetic pathways to the formation of this ring meristem; some of which involve the formation of common petal-stamen mounds prior to, concurrent with, or after ring meristem formation. In most taxa, especially those with high stamen merosity, the stamen primordia are arranged in more or less radial rows (usually ten rows) on the young androecial tubes. Stamen groups (sectorial regions) are generally in line with the petals. Proliferation of stamens generally occurs by partitioning and/or bifurcation in radial, lateral, or oblique directions.

Merosity of the carpels in Malvaceae varies from three to numerous. Carpel number may equal or double the fertile locule number. Depending on the taxon, one to numerous ovules develop in each fertile locule. The ovary is syncarpous and superior with axile placentation. The styles are partially or completely fused into a stylar column. Stigmas (or stigma lobes) are mostly capitate, but may be decurrent or less often wedge-shaped. The gynoecium is exserted (at least slightly) beyond the androecial column at maturity. Prior to or during initiation of the carpels, a low carpel ring meristem may be present or absent. Initiation of the gynoecium usually overlaps with stamen proliferation. Members of the gynoecium may initiate as one or two sets in a single spacial whorl, at least in the taxa I have examined. The initiation sequence within each carpel set is simultaneous. Depending on the taxon, locule differentiation may occur in all or only some of the carpels. Typically, differentiation of ovules and sometimes of the stigmas begins prior to
exsertion of the gynoecium beyond the androecium. An apical residuum is present interior to the young gynoecium.

The fruit type in Malvaceae is a capsule or schizocarp; rarely it is a fleshy schizocarp. The shape of the fruits varies, but in most of the representative taxa width exceeds height. The surface of the fruits may be smooth, rugose, lobed, hairy, or may bear various types of appendages such as spines, lobes, caps, barbs, or wings. The pollen is spheroidal (sometimes oblate to suboblate), polyporate or colporate, and is echinate (one exception is smooth).

Comparison of the three families -- Sterculiaceae, Bombacaceae, and Malvaceae share many features such as valvate sepals, distinct petals, monadelphous or polyadelphous filaments, multicellular glandular hairs localized on the sepals, and a variety of other floral and vegetative characteristics (Cronquist, 1981, 1988). A morphological floral character that separates the Sterculiaceae from the rest of the Malvales is the combination of tetrasporangiate anthers and filaments fused into a tube (Gentry, 1993). Tetrasporangiate anthers are also found in Elaeocarpaceae and Tiliaceae, and a staminal tube in Bombacaceae and Malvaceae, but the combination is unique to Sterculiaceae. In addition, most Sterculiaceae have staminodes and reduced stamen numbers. Bombacaceae are differentiated from most other Malvanean families by fused filaments (a feature shared by Malvaceae), being mostly arborescent (Malvaceae are mostly herbaceous or shrubby), and having pollen that is not spiny (Malvaceae has spiny pollen) (Gentry, 1993). These characters apply in general but there are some notable exceptions. For example, some Malvaceae (*Wercklea, Thespesia, Hampea, Tetrasida, and some Hibiscus*)
are small trees (Ch. 3 and personal observations; Gentry, 1993) and at least one taxon (*Pavonia strictiflora*, formerly *Goethea strictiflora*) has smooth pollen (Ch. 2). *Camptostemon* in the Bombacaceae differs from the usual smooth or textured pollen in the family by having spiny pollen (van Heel, 1966). As previously mentioned, there is a similar wide-range of stamen merosity in Sterculiaceae, Bombacaceae, and Malvaceae, but the overall distribution of stamen numbers varies among the families. This character may be useful at the tribal level in Malvaceae, but without surveying more taxa, its significance at the tribal level in Bombacaceae and Sterculiaceae is in question. Also, the distribution within the stamen merosity range may be helpful at the familial level. Another character that may be of use at the family level is the occurrence of sterile stamens in many Sterculiaceae, but not in Malvaceae (Chs. 2, 3, 4) or in Bombacaceae (van Heel, 1966). This, however, raises the question about whether the staminodes in Sterculiaceae are homologous with the sterile teeth and sterile apical collars found in some Malvaceae and Bombacaceae. Current classification does not use fruit type to delineate the families (although it has been used in the past); there are several fruit types in Sterculiaceae and Malvaceae and two types in Bombacaceae.

These families share several floral ontogenetic characteristics. One consistent feature is helical initiation in the outermost perianth whorl (bractlets or sepals) with a transition to simultaneous initiation of organ sets in the inner floral whorls (petals, stamens, carpels). This means that if sepals are the outermost whorl they initiate helically; but if a helically initiated involucel is present, the sepals may initiate helically or simultaneously. There is no evidence of bidirectional, unidirectional, or spiral (similar to
helical but approaching or receding from the apex) initiation within the floral organ whorls. Helical initiation, however, of floral buds in an inflorescence or of floral bracts may occur. Other important shared characteristics include: partial or complete fusion of the calyx members; petals (when present) are not connate but are usually adnate to the androecium; and presence of some common stamen primordia (in flowers with more than five stamens) that partition and/or bifurcate. In addition, there is overlap in time of initiation of the gynoecia and proliferation of the androecia. The carpels (at least in the taxa I examined) initiate in a single whorl, have an apical residuum interior to the young gynoecium, and form a superior ovary.

One feature that is not consistent within the Malvaceae and perhaps not in the other two families is the presence or absence of ring meristems in the involucels, calices, and gynoecia. Identification of ring meristems in these whorls is complicated because they are often poorly defined, are quickly overtaken by primordia and thus easily missed, and/or sometimes crowding of organ primordia at the time of initiation makes determination difficult. Therefore, presence of a ring meristem is these whorls may not be the most reliable way to distinguish some taxa.

Several ontogenetic and developmental features of the androecium and gynoecium may be useful in delineating the families. In the Malvaceae only one stamen whorl initiates, whereas in the Sterculiaceae most reports describe two whorls. In the Bombacaceae (*Pachira aquatica*) I found two stamen whorls, but previous literature may indicate one or two whorls depending on taxon and investigating method used. In Malvaceae, an androecial ring meristem (in fact a petal-stamen ring meristem) develops. Based on my research and previous literature, an androecial ring meristem
also appears to be common in the Bombacaceae, but not necessarily in the Sterculiaceae. In the Malvaceae there is an obvious enlargement of the ring meristem into a broad tube during stamen proliferation. In Bombacaceae during stamen proliferation the androecium develops into a broad tube as in *Matisia* (Moncur, 1988), *Adansonia*, *Bombax*, and *Ochroma* (van Heel, 1966) or a cup-shaped structure as in *Pachira* (present research; van Heel, 1966). In contrast, the androecial area in Sterculiaceae tends to stay rather flat as in *Herrania sp.* (present research) and *Theobroma* (Bayer and Hoppe, 1990) or to develop into an androgynophore as in *Sterculia* (present research) during stamen proliferation. Although van Heel (1966) had few nonvascular illustrations of Sterculiaceae to analyze, he stated that the mostly united basal part of the androecium develops fully only much later. Another possible difference is that usually in Malvaceae the stamen primordia are arranged in more or less radial rows (at least when high numbers of stamens are present). In the Bombacaceae, the stamens may occupy the entire androecial tube surface as in *Adansonia* (van Heel, 1966), be arranged in radial rows as in *Bombax* (van Heel, 1966) and *Matisia* (Moncur, 1988), or be arranged in clusters or fascicles as in *Pachira* (present research; van Heel, 1966). In *Sterculia*, the stamens appear to be arranged in groups on the androgynophore. The androgynophore is a feature that may be limited to the Sterculiaceae and absent in Malvaceae or Bombacaceae. In the Malvaceae and the Bombacaceae the gynoecium forms a syncarpous ovary and partly or completely fused styles, where as in the Sterculiaceae various degrees of syncarpy and apocarpy occur. Overall, the Bombacaceae appear to share more floral characteristics (both morphological and ontogenetic) with the Malvaceae than do the Sterculiaceae. This judgment, however, is based on
examination of only a few taxa in Sterculiaceae and Bombacaceae and on the very limited ontogenetic data available in previous literature.

**Relative importance of certain characters and familial relationships** — There has been some controversy about whether the large numbers of stamens and/or carpels found in some members of these families in the Malvales reflects a primitive survival or a derived increase (Cronquist, 1981, 1988). Cronquist (1981, 1988) favored the view that polyandry and polycarpy in Malvales is inherited directly from a Thealean ancestry and that there is a phyletic reduction from numerous stamens and carpels to few.

Previous researchers (Payer, 1857; Saunders, 1936; van Heel, 1966) have attempted to attribute the formation of bisporangiate or "half-anthers" in some Malvales to the bifurcation or serial splitting of common stamen primordia. I found in the Malvaceae that bifurcation as well as partitioning do not appear to correlate with the bisporangiate condition (Chs. 2, 3, 4). This is illustrated in many malvaceous taxa in which the bisporangiate condition occurs in stamens that have not undergone any type of furcation event as well as in those that have (Chs. 2, 3, 4). Further evidence that bifurcation is not solely responsible for the bisporangiate condition is found in Sterculiaceae and Bombacaceae. In *Theobroma cacao* (Sterculiaceae) members of only one of the two stamen whorls bifurcate, yet both whorls produce tetrasporangiate anthers (Bayer and Hoppe, 1990; Ronse Decraene and Smets, 1993). I found a similar situation in *Herrania sp.* in which only some primordia of the outer stamen whorl bifurcate, yet all the anthers in this whorl are tetrasporangiate. In *Sterculia ceramicca*, anthers are tetrasporangiate regardless of whether primordia are discretely initiated or
result from partitioning. In *Adansonia digitata* and *Quararibea guianensis* (Bombacaceae) all the stamens initiate as discrete primordia that “do not divide into two halves” (no bifurcation), yet all of the anthers are bisporangiate (van Heel, 1966). So tetrasporangiate anthers develop even if bifurcation and partitioning occur in the Sterculiaceae, and bisporangiate anthers develop in the Bombacaceae and Malvaceae regardless of whether bifurcation occurs. Further proof comes from *Ricinus* (Euphorbiaceae) in that the process of splitting is described as “repeated *ad infinitum*” (Ronse Decraene and Smets, 1993). Therefore, bifurcation and partitioning are simply two means of stamen proliferation and do not determine sporangia number.

Clarification is needed concerning types of sterile structures in the androecia of these three families. In Malvaceae and Bombacaceae the sterile structures (when present) are usually called sterile teeth, sterile appendages, sterile lobes, or less often staminodes or lobules; whereas in the Sterculiaceae the sterile structures (when present) are called staminodes (staminoids or sterile petaloid stamens). It is unclear what the distinction is between the terms sterile teeth and staminodes, and if these terms are applied correctly to the various members of these three families. The sterile parts terminating the androecial tube in some Malvaceae are described as mostly superseded in size by the fertile parts and insignificant as the flower reaches maturity (van Heel, 1966). Yet, some malvaceous taxa (*Malope trifida*, *Sphaeralcea umbellata*, *Lagunaria patersonii*, and *Thespesia populnea*) have well-developed sterile androecial parts that are relatively large at maturity (van Heel, 1966). The staminodes in sterculiaceous taxa are usually conspicuous; but there are exceptions with tiny staminodes, e.g.
Melochia umbellata and Hermannia candicans (van Heel, 1966). Although not typical, some vascularization is found in the sterile teeth of malvaceous taxa, e.g. Kokia rockii and L. patersonii (van Heel, 1966) and in two varieties of Hibiscus rosa-sinensis (Saunders, 1936). The staminodes in most Sterculiaceae are described as vascularized, but there are a few exceptions (van Heel, 1966). So there does not appear to be a clear distinction between the sterile androecial structures in these families based on size or vasculature, but rather there appears to be gradation in size and amount of vasculature in the structures. Position of the sterile androecial structures is another issue. It was suggested that the sterile teeth in Malvaceae are the terminations of the antepetalous stamen whorl and that all traces of the antesepalous whorl are suppressed (Saunders, 1936). A contrary view would be that the sterile androecial parts are remnants of an inner stamen whorl in Malvaceae. Neither of these interpretations, however, can be used to generalize sterile androecial structures in all malvaceous taxa since the position of these structures varies among Malvaceae, being either antepetalous or alternipetalous (Ch. 2; van Heel, 1966) and sharing the same radii or not with the first-whorl stamen groups (Ch. 2). Also, Bombax buonopozense, B. ceiba, and B. ellipticum (Bombacaceae) have been described with sterile apical collars or sterile apical teeth in addition to two stamen whorls (van Heel, 1966). Obviously more research (position as well as vasculature and size) is needed to resolve homologies among these structures.

According to Cronquist (1981) there has been some dispute over whether the more or less apocarpous flowers in the tribe Sterculieae are primitive or not within the Sterculiaceae. One interpretation is that apocarpy
is an ancestral condition that survives in some of the higher advanced angiosperms groups (Stebbins, 1974). The opposing opinion would be that apocarpy in some members of the Sterculiaceae is probably derived rather than primitive within the family (Cronquist, 1981). Cronquist (1981) based the latter hypothesis on the temporary fusion of styles in Sterculia at anthesis and a similar evolutionary trend in Apocynaceae and Asclepiadaceae, in which there is a phyletically progressive separation of the carpels from the bottom upwards. Endress, Jenny, and Fallen (1983) concur that evolution may have occurred from syncarpy to apocarpy in Sterculiaceae, especially with the temporary postgenital fusion of apical and subapical parts to form a common pollen tube transmitting tissue, a compitum, at anthesis. They stated, contrary to Cronquist, that the trend towards apocarpy takes place with progressive separation of the gynoecia from top to bottom in Loganiaceae, Apocynaceae, and Asclepiadaceae.

Floral ontogeny (with the advancement of SEM) is a useful tool to clarify the formation of floral structures and will add to our knowledge about similarities and differences among taxa. It may also prove to be useful in determining homologies of certain structures. The evolutionary aspects of ontogenetic characters in the Malvales will be explored in a future cladistic analysis (Ch. 6).

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CHAPTER 6
PHYLOGENETIC ANALYSIS OF MALVACEAE USING ONTOGENETIC AND MORPHOLOGICAL CHARACTERS

INTRODUCTION

Opinions have often differed regarding delimitations of species, genera, and tribes in the large plant family Malvaceae (Edlin, 1935; Kearney, 1951; Hutchinson, 1967; Bates, 1968; Fryxell, 1968, 1997). Recently, cladistic studies have attempted to clarify the phylogeny in the Malvaceae (Fryxell and La Duke, 1994; La Duke and Doebley, 1995; Ray, 1995; Seelanan, Schnabel, and Wendel, 1997), in the Malvales (Judd and Manchester, 1997; Alverson et al., 1998, 1999; Baum, Alverson, and Nyffeler, 1998; Bayer et al., 1999), and in the Rosidae or higher (Chase et al., 1993; Alverson et al., 1998; APG, 1998). These studies have used molecular data (Chase et al., 1993; La Duke and Doebley, 1995; Ray, 1995; Seelanan, Schnabel, and Wendel, 1997; Alverson et al., 1998, 1999; Baum, Alverson, and Nyffeler, 1998; APG, 1998; Bayer et al., 1999) or various types of morphological data (Fryxell and La Duke, 1994; Ray, 1995; Judd and Manchester, 1997), but none have included ontogenetic floral data. Previous studies (Tucker, Douglas, and Liang, 1993; Tucker and Douglas, 1994, 1996) have shown that floral ontogenetic data can be helpful in resolving phylogenetic relationships in other plant families. Therefore, cladistic analyses will be performed using a combination of floral ontogenetic characters and various morphological characters in an attempt to add insight into the phylogeny of the Malvaceae, to test the monophyly of four of the
currently recognized tribes, and to examine some of the intergeneric relationships in the family.

The number of genera placed in Malvaceae has varied greatly over the years, but recent estimates place the number at approximately 141 (Ch. 1). Early treatments of the family were described by Baillon (1875), Maout and Decaisne (1876), Schumann (1891), Edlin (1935), Kearney (1951), Benson (1957), and Engler (1964). Edlin (1935) moved the Hibisceae (which included *Howittia*) and Kydieae (*Kydia*) tribes to the Bombacaceae so that Malvaceae included only schizocarpous fruits. Kearney (1951) reevaluated the American genera of Malvaceae and recognized four tribes, Hibisceae, Ureneae, Malopeae, and Malveae. The Malveae was further subdivided into the subtribes Corynabutilinae, Malvinae, Abutilinae, and Sidinae. The major difference between Kearney's (1951) treatment and Hutchinson's (1967) is the addition of Old World genera. In addition, Hutchinson removed two subtribes, Abutilinae and Sidinae, from Malveae and placed them into a fifth tribe called Abutileae. Bates (1968) studied the Malveae and claimed the earlier systems overemphasized a few key characters, mainly gynoecial characters, and suggested a system based largely on a number of correlated characters from morphology, cytology, and phytogeography. He combined Malopeae into Malveae and therefore recognized three major tribes of Malvaceae: Malveae, Hibisceae, and Ureneae. He also pointed out that *Kydia* and *Howittia* do not fall easily into any one tribe as currently defined. Bates (1968) and Bates and Blanchard (1970) further subdivided Malveae into informal groups called "alliances". In 1968, Fryxell resurrected and redefined the tribe Gossypieae, separating it from the Hibisceae. The genus *Decaschistia* was removed from Hibisceae.
and placed in a tribe of its own, Decaschistieae (Fryxell, 1975). The older name Malvavisceae was resurrected for the tribe otherwise known as Ureneae or Pavonieae (Fryxell, 1988). Subsequently, the genera included in Malvavisceae, in particular *Pavonia*, were redefined (Fryxell, 1997, 1999). In 1997, Fryxell described the American genera of Malvaceae, taking into account the more than 20 new genera since Kearney's (1951) treatment and numerous revisions, expansions, narrowings, and reinterpretations of existing genera. In this treatment, *Kydia* is placed in the Malvaceae. Currently, the five tribes recognized in the Malvaceae are Gossypieae, Hibisceae, Malvavisceae, Malveae, and Decaschistieae (Fryxell, 1988).

Malvaceae is closely allied with the other core families in the Malvales (Sterculiaceae, Bombacaceae, and Tiliaceae); and there has often been controversy about their interfamilial limits (Edlin, 1935; Bates, 1968; Fryxell, 1968; Cronquist, 1988; Judd and Manchester, 1997; Bayer et al., 1999). Recently, it has been proposed that the Malvaceae be expanded to comprise all core Malvales and subdivided into various subfamilies (Judd and Manchester, 1997; APG, 1998; Baum, Alverson, and Nyffeler, 1998; Bayer et al., 1999) and that Malvales be expanded to include additional families (Dahlgren, 1980; Thorne, 1992; APG, 1998; Baum, Alverson, and Nyffeler, 1998; Alverson et al., 1998, 1999; Bayer et al., 1999). Most cladistic analyses are in agreement that even though the traditionally circumscribed sister families are not monophyletic, Malvaceae (in the strict sense) appears to be monophyletic (Judd and Manchester, 1997; Baum, Alverson, and Nyffeler, 1998; Alverson et al., 1999; Bayer et al., 1999). Malvaceae s. str. is either placed as the most advanced in the order with the other core families positioned variously in closely related basal positions (Chase et al., 1993;
Judd and Manchester, 1997; Baum, Alverson, and Nyffeler, 1998; Alverson, 1998, 1999) or as paraphyletic with the other core families (Baum, Alverson, and Nyffeler, 1998; Bayer et al., 1999). Therefore, representatives of the Bombacaceae and Sterculiaceae have been chosen as outgroup taxa for the present analysis of the traditionally circumscribed Malvaceae.

This paper presents the results of a preliminary cladistic analysis of the Malvaceae s. str. Ontogenetic floral characteristics in addition to various morphological characters are included in this analysis. Selected representatives of each tribe in the Malvaceae (excluding Decaschistieae), as well as outgroup taxa, have been examined. This study will attempt to advance understanding of the phylogeny of the Malvaceae and test the monophyly of groups (tribes) in the Malvaceae.

**MATERIALS AND METHODS**

Twenty-six taxa were selected for this analysis; 22 in Malvaceae, three in Sterculiaceae, and one in Bombacaceae (Table 6.1). Prior to cladistic studies, the malvaceous taxa chosen for this analysis have generally not been in question as far as their placement in current tribes. An effort was made to include both temperate and tropical representatives in the Malvaceae. In addition, the type genus of each tribe in Malvaceae (excluding Decaschistieae) is represented in this analysis.

Ontogenetic floral data were obtained for 24 species from floral developmental studies by this author (Chs. 2 - 5). These studies utilized scanning electron microscopy (SEM) and light microscopy techniques. In addition, fairly complete developmental series with SEM have been published for *Hibiscus acetosella* (Ault, 1987) and *Theobroma cacao* (Bayer and Hoppe, 1990); thus these two species have also been included in this
cladistic analysis. Most mature floral and vegetative characteristics were obtained by examination of FAA-ethanol preserved material and herbarium specimens by this author (Table 6.1). Literature was also used to verify and supplement species information (Table 6.1).

The analysis included 88 characters; of these 55 are binary and 33 are multistate (Table 6.2). The data matrix (Table 6.3) was assembled using MacClade, version 3.01 (Maddison and Maddison, 1992). All characters were unordered, unpolarized, and equally weighted. The matrix included some autapomorphic characters. These characters were incorporated in the current study because they are found in other excluded members of the Malvales, i.e. they may be typical of an entire genus or found in several genera. So, even though autapomorphic characters are not informative about evolutionary relationships in the current preliminary analysis, as more taxa are added to the matrix the characters may become informative. Presently, it can be expected that the autapomorphies will increase the number of tree steps, but will not affect tree topography. In addition, these uninformative characters can be excluded from the consistency and homoplasy indices by the current cladistic program.

Parsimony analyses were performed with PAUP, version 3.1.1 (Swofford, 1993) on a Macintosh Performa 6116CD. All multistate entries in the data matrix were treated as polymorphisms. The data were analyzed using delayed transformation (DELTRAN) optimization. The searches used the heuristic algorithm with stepwise addition of 1000 random replicates and branch swapping by tree-bisection-reconnection (TBR) with multiple parsimony (MULPARS). Other parameters include: keep minimal trees only, swap on minimal trees only, and collapse 0-length branches. All trees were
**TABLE 6.1.** List of Malvolean taxa, vouchers, and references examined to compile data for cladistic analyses.

<table>
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<tr>
<th>Taxon</th>
<th>Voucher</th>
<th>Reference**</th>
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<td><em>Callirhoe involucrata</em></td>
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<td><em>Liamnaremota</em></td>
<td>TSC-0110</td>
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<td>TSC-0079</td>
<td>8, 13</td>
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<td><em>Pachira aquatica</em></td>
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(Table continued)
a *Malvaviscus arboreus* var. *drummondii*.
b *Pavonia strictiflora* (= *Goethea strictiflora*).
c This collection of *Abelmoschus manihot* is atypical in having ten carpels per gynoecium.
d *Gossypium hirsutum* cultivar DPL50.
e *Callirhoe involucrata* var. *involucrata*.

* Complete voucher information is available in Chs. 2 - 5, except TSC-0067 (*Hibiscus acetosella*, grown at Hill Farm/Louisiana State University, Baton Rouge, LA, US, seeds from The Flowery Branch, by T. Crozier, Nov. 1992) and TSC-0120 (*Theobroma cacao*, growing in climatron at Missouri Botanical Gardens, St. Louis, MO, US, MOBOT# 890691, by T. Crozier, Oct. 1993). All of the TSC series vouchers are currently held by this author.

TABLE 6.2. Characters and character states used in cladistic analysis of the Malvaceae.

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<thead>
<tr>
<th>Character Description</th>
<th>State 0</th>
<th>State 1</th>
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<tbody>
<tr>
<td>1. Habit:</td>
<td>0 = small to large tree; 1 = shrub, subshrub, or shrublet; 2 = herbaceous.</td>
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<tr>
<td>2. Stem orientation:</td>
<td>0 = erect; 1 = not erect.</td>
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<td>3. Life cycle:</td>
<td>0 = perennial; 1 = annual.</td>
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<tr>
<td>4. Leaf complexity:</td>
<td>0 = simple; 1 = palmately compound; 2 = pinnately compound.</td>
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<td>5. Foliar nectaries on veins of abaxial leaf surface:</td>
<td>0 = absent; 1 = present.</td>
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<tr>
<td>6. Stipular nectaries at base of petiole in conjunction with two stipules:</td>
<td>0 = absent; 1 = present.</td>
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<tr>
<td>7. Floral nectaries, nontrichomatous, in area of outer receptacle, i.e. below outer sepals or bractlet bases:</td>
<td>0 = absent; 1 = present.</td>
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<tr>
<td>8. Sepal trichomatous nectaries:</td>
<td>0 = inner sepal bases; 1 = inner sepal apices.</td>
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<tr>
<td>9. Gossypol glands:</td>
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<td>10. Inflorescence position:</td>
<td>0 = with leafy shoots; 1 = arising from bark.</td>
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<tr>
<td>11. Number of flowers in an inflorescence:</td>
<td>0 = one; 1 = variable, one to many; 2 = numerous.</td>
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<td>12. Pedicels elongate:</td>
<td>0 = elongated; 1 = not elongated, capitulum.</td>
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<tr>
<td>13. Pedicel articulation in floral development:</td>
<td>0 = nonjointed; 1 = jointed.</td>
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<tr>
<td>14. Flower shape:</td>
<td>0 = open, flared; 1 = tubular.</td>
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<tr>
<td>15. Floral bracts:</td>
<td>0 = absent; 1 = present.</td>
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<tr>
<td>16. Bractlet development:</td>
<td>0 = none initiated; 1 = initiated then suppressed or caducous; 2 = initiated and developed to anthesis.</td>
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<tr>
<td>17. Bractlet color:</td>
<td>0 = green; 1 = other than green.</td>
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<tr>
<td>18. Bractlet position:</td>
<td>0 = one whorl immediately adjacent to calyx; 1 = variously spaced below the calyx.</td>
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<tr>
<td>19. Bractlet merosity:</td>
<td>0 = zero; 1 = three; 2 = four; 3 = five; 4 = variable, four to numerous.</td>
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<tr>
<td>20. Bractlet fusion (connexion) at anthesis:</td>
<td>0 = no fusion; 1 = fused less than half length; 2 = fused half or more length.</td>
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<tr>
<td>21. Bractlets apically forked:</td>
<td>0 = absent; 1 = present.</td>
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<tr>
<td>22. Bractlet ring meristem:</td>
<td>0 = absent; 1 = present.</td>
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<tr>
<td>23. Bractlet order of initiation:</td>
<td>0 = helical distinct primordia; 1 = helical common primordia.</td>
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<tr>
<td>24. Sepal merosity:</td>
<td>0 = five; 1 = typically four (less often three or five).</td>
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<tr>
<td>25. Sepal color:</td>
<td>0 = green; 1 = other than green.</td>
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</tr>
<tr>
<td>26. Sepal length:</td>
<td>0 = greater than bractlets or floral bracts if bractlets are lacking; 1 = approximately equal to bractlets (or floral bracts); 2 = less than bractlets (or floral bracts).</td>
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(Table continued)
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<tr>
<td>27.</td>
<td>Sepal fusion, amount at anthesis: 0 = less than half length; 1 = half to more length but not completely; 2 = completely or nearly so; 3 = not fused.</td>
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<tr>
<td>28.</td>
<td>Calyx vertically ribbed in early development: 0 = not ribbed, nearly smooth; 1 = prominently ribbed.</td>
</tr>
<tr>
<td>29.</td>
<td>Sepal ring meristem: 0 = absent; 1 = present.</td>
</tr>
<tr>
<td>30.</td>
<td>Sepal order of initiation: 0 = helical; 1 = simultaneous.</td>
</tr>
<tr>
<td>31.</td>
<td>Sepal apices in bud: 0 = meet at top of dome; 1 = extend beyond dome.</td>
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<tr>
<td>32.</td>
<td>Petal color: 0 = white, cream, pale green; 1 = yellow, orange, orange-red; 2 = red, pink, maroon, lavender, purple.</td>
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<tr>
<td>33.</td>
<td>Petal base color spot: 0 = absent; 1 = present.</td>
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<tr>
<td>34.</td>
<td>Petal length compared to sepals: 0 = approximately equal; 1 = exceed sepals.</td>
</tr>
<tr>
<td>35.</td>
<td>Petal bases: 0 = lacking auricles and ciliate tufts; 1 = have auricles; 2 = have ciliate tufts on lateral margins of claw.</td>
</tr>
<tr>
<td>36.</td>
<td>Petals hooded with apical appendages: 0 = absent; 1 = present.</td>
</tr>
<tr>
<td>37.</td>
<td>Petal merosity: 0 = zero; 1 = five.</td>
</tr>
<tr>
<td>38.</td>
<td>Common petal-stamen mounds: 0 = absent; 1 = present.</td>
</tr>
<tr>
<td>39.</td>
<td>Petal elongation timing: 0 = not delayed; 1 = delayed until individual stamens have initiated.</td>
</tr>
<tr>
<td>40.</td>
<td>Timing of petal initiation: 0 = concurrent with first common stamen; 1 = after stamen proliferation underway.</td>
</tr>
<tr>
<td>41.</td>
<td>Stamen merosity: 0 = 50 or less; 1 = between 50 and 100; 2 = more than 100.</td>
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<tr>
<td>42.</td>
<td>Twisting of androecial column: 0 = absent; 1 = present.</td>
</tr>
<tr>
<td>43.</td>
<td>Androecial exsertion: 0 = included in corolla (perianth); 1 = exserted beyond corolla.</td>
</tr>
<tr>
<td>44.</td>
<td>Stamen level of divergence: 0 = throughout column; 1 = upper portion of column; 2 = apical on column.</td>
</tr>
<tr>
<td>45.</td>
<td>Androecial symmetry: 0 = actinomorphic, stamens displayed radially; 1 = zygomorphic, stamens secund (bend to one side of the column).</td>
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<tr>
<td>46.</td>
<td>Stamen filaments retrorse at anthesis: 0 = not retrorse; 1 = retrorse.</td>
</tr>
<tr>
<td>47.</td>
<td>Stamen filament development: 0 = anthers sessile or nearly so; 1 = filaments elongated.</td>
</tr>
<tr>
<td>48.</td>
<td>Sporangia per anther: 0 = two; 1 = four.</td>
</tr>
<tr>
<td>49.</td>
<td>Androecial ring meristem: 0 = absent; 1 = present.</td>
</tr>
<tr>
<td>50.</td>
<td>Timing of androecial tube development: 0 = during stamen proliferation to early differentiation; 1 = after stamen differentiation is well underway.</td>
</tr>
</tbody>
</table>

(Table continued)
51. Sequence of early androecial initiation: 0 = ring meristem, then petal-stamen common mounds; 1 = ring meristem and petal-stamen mounds concurrently; 2 = petal-stamen mounds, then ring meristem; 3 = ring meristem only, no common petal-stamen mounds; 4 = no ring meristem.

52. Partitioning direction in androecium: 0 = only lateral; 1 = lateral and centrifugal; 2 = lateral, centrifugal, and centripetal; 3 = variable pattern; 4 = no partitioning after five primordia.

53. Direction of furcation in the androecium: 0 = lateral to obliquely lateral; 1 = radial to obliquely radial; 2 = variable; 3 = no furcation.

54. Androecial primordia arranged in radial rows: 0 = not in rows; 1 = approximately ten rows; 2 = approximately 20 rows.

55. Androecial first whorl position: 0 = opposite petals; 1 = alternate to petals; 2 = intermediate, off-alternate or off-opposite petals.

56. Number of stamen whorls: 0 = one; 1 = two.

57. Androecial whorl arrangement: 0 = only one whorl initiated; 1 = two whorls initiated in same spatial whorl; 2 = two whorls initiated spatially separated, one interior and one exterior.

58. Prominent sterile stamen: 0 = absent; 1 = present.

59. Fertile stamen types: 0 = one type; 1 = two types.

60. Androecial meristematic pads: 0 = absent; 1 = present.

61. Androecial meristematic pad positions: 0 = absent; 1 = abaxial and vertical on the tube; 2 = adaxial and sloped on the tube.

62. Sterile androecial teeth development: 0 = not initiated; 1 = initiated then suppressed; 2 = initiated then developed to anthesis.

63. Sterile androecial teeth at maturity: 0 = absent; 1 = present.

64. Sterile androecial teeth positions: 0 = opposite petals; 1 = intermediate, opposite to alternate to the petals; 2 = alternate to petals.

65. Number of carpels initiated: 0 = three; 1 = variable three to five; 2 = five; 3 = ten; 4 = variable five to 25.

66. Carpel fertility: 0 = all carpels form fertile locules; 1 = only half of carpels form fertile locules.

67. Locule development in sterile carpels: 0 = N/A, all carpels fertile; 1 = rudimentary locule development; 2 = no locule development.

68. Ovule number per locule: 0 = one; 1 = two; 2 = three; 3 = variable two to many; 4 = variable and numerous.

69. Ovary fusion: 0 = syncarpous; 1 = apocarpous.

70. Stylar fusion: 0 = styles fused entire length; 1 = styles partially fused; 2 = styles unfused.

71. Stylar exsertion: 0 = exserted past androecium; 1 = included in androecium.

72. Number of carpel sets (whorls): 0 = one; 1 = two.
73. Carpel ring meristem: 0 = absent; 1 = present.
74. Androgynophore: 0 = absent; 1 = present.
75. Stigma type: 0 = capitate, convex; 1 = extrorsely decurrent; 2 = introrsely decurrent; 3 = wedge shaped, introrsely.
76. Placentation: 0 = axile; 1 = marginal.
77. Fruit type: 0 = fleshy, berry-like; 1 = schizocarp; 2 = capsule; 3 = group of follicles.
78. Fruit dimensions: 0 = width greater than to equal length; 1 = width less than to equal length.
79. Fruit dehiscence: 0 = indehiscent; 1 = loculicidally dehiscent; 2 = septicidally dehiscent.
80. Fruit surface texture: 0 = relatively smooth or softly pubescent; 1 = spines to long stiff hairs; 2 = barbs; 3 = rugose, reticulate, striate.
81. Fruit cross section outline: 0 = circular; 1 = vertically ribbed or grooved; 2 = angled; 3 = lobed; 4 = pod-like, vertically flattened.
82. Fruit central disk: 0 = absent to inconspicuous; 1 = present and prominent.
83. Fruit apical cap: 0 = absent; 1 = present.
84. Fruit appendages: 0 = absent; 1 = apical lobes; 2 = apical spines; 3 = apical beak or apically pointed; 4 = lateral wings.
85. Pollen shape: 0 = spheroidal to spherical; 1 = oblate to suboblate; 2 = prolate.
86. Pollen aperture type: 0 = porate; 1 = colporate.
87. Pollen aperture number: 0 = three; 1 = variable two to 15; 2 = variable 20 to numerous.
88. Pollen surface texture: 0 = spiny; 1 = not spiny.
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<th>Taxon</th>
<th>Character number</th>
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*Abbreviation Anisodontea X hypomandarum.

Polymorphic character states are indicated by the AND separator (e.g. 0&1). Partially uncertain character states are indicated by OR separator (e.g. 0/2, indicates it may be 0 or 2, but not any other character states such as 1). Entirely uncertain states are indicated with the missing data symbol (?). The gap symbol (-) is used to indicate that the character does not apply to the species, for example characteristics of the bractlets when bractlets are lacking.
rooted using an outgroup with options making the ingroup monophyletic and the outgroup paraphyletic. An analysis was performed with both bombacaceous and sterculaceous taxa selected as the outgroup. A strict consensus tree was calculated in PAUP and characters were traced on the tree using MacClade.

Preliminary analyses were also performed using accelerated transformation (ACCTRAN) optimization on similar data sets to determine if favoring reversals over parallelisms changes tree topography. In addition, analyses were conducted using DELTRAN with only the sterculaceous taxa as the outgroup, and then with only the Bombacaceae representative as the outgroup; thus ingroup stability could be assessed relative to outgroup choice.

Bootstrap analysis of the data was performed to test the relative frequency of well-supported clades within the data matrix. The bootstrap used heuristic algorithm with 100 repetitions and one random number seed. The parameters were the same as in the previous analysis except stepwise addition with one random replication. All groups compatible with 50% majority-rule consensus were retained in the bootstrap consensus tree. Attempts to do decay analyses were aborted due to insufficient computer memory.

**RESULTS**

Parsimony analysis with DELTRAN optimization and using both Bombacaceae and Sterculiaceae as the outgroup produced five equally parsimonious trees of 328 steps. The following PAUP statistics apply to these trees: consistency index (CI) = 0.585, CI excluding uninformative characters = 0.477, homoplasy index (HI) = 0.582, HI excluding uninformative
characters = 0.616, retention index (RI) = 0.632, and rescaled consistency index (RCI) = 0.370. The strict consensus derived from these trees is shown in Fig. 6.1. The five most parsimonious trees differ only in placement of taxa within the Malveae clade. Therefore, only excerpts from these trees which show the differing topographies of the Malveae clade are illustrated (Figs. 6.2 - 6.6) along with the majority-rule consensus (Fig. 6.7).

Within the Malvaceae s. str., only three of the four commonly recognized tribes are supported as discrete groups. Malvaceous taxa are divided into two large subgroups, one with members of the Malveae and the other consisting of the remaining three major tribes (excluding Decaschistieae). Members of the Malvavisceae form a clade and are part of a larger clade which includes members of the Hibisceae and ultimately the Gossypieae. Members of the Hibisceae are paraphyletic. Gossypieae and the Malveae are both monophyletic. Within the Malvavisceae clade, *Malvaviscus* and *Pavonia* are more recently evolved than *Malachra* and *Urena*. *Gossypium* and *Thespesia* are more closely allied than *Cienfuegosia*. The strict consensus tree (Fig. 6.1) and the majority-rule consensus (Fig. 6.7) show the unresolved polytomy within the Malveae clade. The bombacaceous taxon, *Pachira*, is more closely allied with the Malvaceae than the sterculiaceous representatives.

The preliminary analyses utilizing ACCTRAN optimization produced comparable trees (same topographies, tree lengths, and statistics) to those with DELTRAN. Similarly, designation of just Bombacaceae or just Sterculiaceae taxa as the outgroup did not change the topography of the malvaceous ingroup; and the nondesignated outgroup is never nested.
within the ingroup. Therefore, cladograms produced by these analyses are not illustrated.

Bootstrap analysis (Fig. 6.8) shows good support (89%) for the Malvavisceae clade and moderate support (47 - 66%) for the positions of taxa within the tribe. The inclusion of Malvavisceae with the Hibisceae and Gossypieae into a larger clade is very tentative. In the bootstrap tree, there is weak support for *Abelmoschus* and the two *Hibiscus* species forming a clade and for the other members of Hibisceae as paraphyletic. Gossypieae as a clade is poorly supported with only 38% bootstrap value, but the association between *Gossypium* and *Thespesia* is more strongly supported with 64%.

The Malveae clade has a bootstrap value of only 60%. Similar to the majority-rule consensus tree, bootstrap values show modest support for the association of the sister taxa *Abutilon* and *Sida*.

Characters that uniquely support the Malvavisceae clade are the initiation of two carpel sets (char. 72) and the development of both sterile and fertile carpels in the gynoecium (chars. 66, 67). Having ten carpels in the gynoecium is also restricted to this clade except for the aberrant collection of *Abelmoschus* (char. 65, Fig. 6.11). Other characters that help to support Malvavisceae as a clade but are not unique to the group include: stamens diverge from upper portion of column (char. 44), furcation only in radial to obliquely radial directions (char. 53), one ovule per locule (char. 68), and schizocarpic fruit (char. 77, Fig. 6.12).

The large clade which includes both Malvavisceae and Hibisceae is supported by the lack of ciliate tufts on petal bases (char. 35) and by initiation of an androecial ring meristem followed by common petal-stamen mounds (char. 51, Fig. 6.10). In addition, all of the members of this group, except...
*Malachra*, have more than three bractlets (char. 19, Fig. 6.9). It should be noted that various members of the Hibisceae share an assortment characteristics not only with the Malvavisceae, but also with the Gossypieae.

Gossypieae is unique with the presence of gossypol glands (char. 9) and with carpel numbers of three or variable between three and five (char. 65, Fig. 6.11). Other characteristics that help to delineate the tribe but are also present outside the group include: three bractlets (char. 19, Fig. 6.9), stamen divergence throughout the length of the androecial column (char. 44), styles that are fused their entire length (char. 70), capsular fruit (char. 77, Fig. 6.12), and possibly the initiation of a carpel ring meristem (char. 73).

The lack of sterile androecial teeth in mature flowers (char. 63) has long been used to delineate the Malveae tribe, though it should be noted that some members initiate, then suppress sterile teeth (char. 62). The clade is also supported by carpel numbers which vary between five and 25 (char. 65, Fig. 6.11) and, to a lesser extent, by sepals greater in length than the bractlets (char. 26), styles partially fused (char. 70), initiation of a carpel ring meristem (char. 73), and schizocarpic fruit (char. 77, Fig. 6.12).

The outgroup taxa are separated from the Malvaceae by having two whorls of stamens (char. 56). To a lesser extent they are also distinguished by habit, with the Malvaceae being mostly herbs or shrubs and the outgroups mostly trees (char. 1), and by pollen surface texture, with malvaceae having mostly spiny pollen and the outgroups mostly smooth pollen (char. 88). Characters that are found in some of the outgroup taxa but not in the malvaceous ingroup include: compound leaves (char. 4), inflorescences arising from bark (char. 10), hooded petals (char. 36) or absence of petals (char. 37), tetrasporangiate anthers (char. 48), lack of a ring meristem (char.
Fig. 6.1. Strict consensus tree of five equally most parsimonious trees based on ontogenetic and morphological data. Trees have 328 steps. The heuristic search used DELTRAN optimization and tree rooting by outgroup. Malvaceae tribal abbreviations: MVS = Malvaviscae, HIB = Hibisceae, GOS = Gossypieae, MVA = Malveae. Outgroup abbreviations: STC = Sterculiaceae, BOM = Bombacaceae.
Figs. 6.2 - 6.7. Topographies for the Malveae clade. Figs. 6.2 - 6.6 are exserts from the five equally most parsimonious trees using ontogenetic and morphological data. Fig. 6.7. is an exsert from the majority-rule consensus tree. Numbers above the lines are majority-rule consensus values. Total length of entire trees (including other clades as in Fig. 6.1) = 328 steps. Only genus names are used to indicate the specimens used in the analysis.
Fig. 6.8. Bootstrap tree generated with ontogenetic and morphological data and using a heuristic algorithm with 100 replicates. Tree length = 314 steps. Numbers above the lines indicate bootstrap values.
Fig. 6.9. Tracing of number of bractlets initiated, character 19, on strict consensus tree. *Pavonia strictiflora* is polymorphic for this character, having four bractlets or less often only three.
Fig. 6.10. Tracing of sequence of early androecial initiation, character 51, on strict consensus tree. Character states (shown abbreviated in the key) are as follows: state 0 = initiation of a ring meristem prior to initiation of common petal-stamen mounds; state 1 = a ring meristem initiates concurrent with petal-stamen mounds; state 2 = initiation of common petal-stamen mounds prior to a ring meristem; state 3 = initiation of a ring meristem without common petal-stamen mounds; state 4 = no ring meristem initiates. Taxon states marked as uncertain are as follows: *Urena lobata* = 0/1, *Abelmoschus manihot* = 0/3, *Radyera farragei* = 0/1, *Thespesia populnea* = 0/3, *Callirhoe involucrata* = 0/3.
Fig. 6.11. Tracing of number of carpels initiated, character 65, on strict consensus tree. The collection of *Abelmoschus manihot* included in this analysis is aberrant in having ten carpels; this genus and species typically have a five-merous gynoeceum.
Fig. 6.12. Tracing of fruit type, character 77, on strict consensus tree. The fruit type in Pavonia strictiflora is not known.
49), delayed elongation of the androecial tube (char. 50), development of sterile stamens (char. 58), presence of androecial meristematic pads (char. 60), gynoecium included in the androecium (char. 71), presence of an androgynophore (char. 74), and marginal placentation (char. 76). With examination of more taxa in future analyses, some of these distinctions may become nonapplicable.

Several evolutionary trends are apparent in this analysis. Bractlet number tends to increase from zero (in the sterculiaceous representatives) to three (in the bombacaceous taxon, the Gossypieae, and most Malveae) to mostly four or more (in Hibisceae + Malvavisceae) (Fig. 6.9). Bractlets have been lost in a few taxa. Primitive carpel number appears to be five with a progression to fewer in the Gossypieae clade and to more numerous in the Malvavisceae and Malveae lineages (Fig. 6.11). Ovule number exhibits an overall reduction pattern (char. 68). Outgroup taxa, Gossypieae, and most of the Hibisceae have variable ovule numbers between two and many or even numerous per locule. The Malveae clade is diverse for this character with ovule numbers of one two, three, or variable. The Malvavisceae + Kosteletzkya possess one ovule per locule. Though not well defined, transitions occur in pollen apertures from colporate to porate (char. 86) and in pollen aperture number from three to variable (with numbers ranging from two to numerous) (char. 87). Schizocarpic fruits appear to have evolved twice in the Malvaceae, though this observation may be due to the somewhat ambiguous placement of the Hibisceae members (Fig. 6.12). The early sequence of androecial initiation varies among taxa in this analysis. There appears to be a general trend in androecial development from: either not having a ring meristem or the initiation of common petal-stamen mounds then
development of a ring meristem -> initiation of the ring meristem concurrent with common petal-stamen mounds or just initiation of the ring meristem without common mounds -> initiation of a ring meristem prior to initiation of common petal-stamen mounds (Fig. 6.10). Stamen merosity (char. 41) is homoplastic, though the more highly derived taxa, Malvavisceae + Kosteletzkya, all have low numbers (50 or less). It should be noted that these evolutionary trends apply to the Malvaceae and do not necessarily reflect overall trends in the order. The mapping of these characters may change as more ingroup and outgroup taxa are added to the analysis.

**DISCUSSION**

Several hypotheses have been formulated by previous researchers regarding the phylogeny of tribes in the Malvaceae. Hutchinson (1967) postulated, based on gynoecial characters, that Malopeae (now included in the Malveae) is the most primitive tribe and that Ureneae (now Malvavisceae) is probably the most highly evolved tribe. Both Bates (1968) and Christensen (1986) stated that tribal divergence probably occurred early in the history of the family. Bates (1968), with his three-tribe system (Malveae, Hibisceae, and Ureneae), stated that "there is no compelling reason to believe that any of the three is ancestral to another." His theory was supported by the widespread distribution and by the diversity of morphological and cytological forms comprising each tribe. Based on pollen morphology, Christensen (1986) hypothesized that Malveae (including Malopeae) and Abutileae (now in Malveae) had a long and distinct evolutionary history and that Hibisceae and Ureneae (Malvavisceae) should be regarded as very close to one another. In my analysis, Hibisceae and Malvavisceae are closely related and Malvavisceae appears to be the most highly derived tribe. The Malveae
clade branches off from a more basal position on the tree than the other tribes. Not enough taxa were examined in the large Malveae tribe to determine subtribal affinities.

Tree topographies obtained in these analyses are similar in several respects to those obtained by La Duke and Doebley (1995) with chloroplast DNA data. Both our analyses divide the Malvaceae into two large subgroups, one consisting of Malveae and the other consisting of the remaining three tribes (excluding Decaschistieae). Gossypieae and Malveae are both monophyletic, and in La Duke and Doebley’s analysis these clades are strongly supported by bootstrap and decay values. Although their analysis does not support the monophyly of the Malvavisceae, it does show the paraphyly of the Hibisceae between members of the Malvavisceae and the Gossypieae. Their trees also show the association between the sister taxa *Malaviscus* and *Pavonia*, *Gossypium* and *Thespesia*, and *Abutilon* and *Sida*.

Similarly, Fryxell and La Duke (1994) stated that there is clear separation of Malveae, based on their large cladistic analysis of the Malvaceae with morphological data. Their trees support the integrity of the Malvavisceae and Gossypieae clades and that the Hibisceae are intact to a lesser extent.

Two analyses of the core Malvales, which included only a limited number of malvaceous taxa, have somewhat contradictory results to mine and the two aforementioned studies. Judd and Manchester (1997) used morphological, anatomical, palynological, and chemical characters in their data matrix. They described Gossypieae (one genus represented) as most basal in the order and Hibisceae (one genus represented) as the sister group
to the Malveae + Malvavisceae. Both Malvavisceae (two genera represented) and Malveae (three genera represented) formed clades and were positioned as most advanced in the family. Alverson et al. (1999), with ndhF sequence data, illustrated the Malvaceae s. str. divided into two large clades, but with one consisting of Malveae (two species represented) + Gossypieae (three species represented) and the other of Malvavisceae (two species represented) + Hibisceae (one species represented). In their consensus tree, only Gossypieae and Malvavisceae are monophyletic.

Placement of some taxa are of particular interest. Abelmoschus was formerly submerged in Hibiscus, but it is now generally treated as distinct (Kearney, 1951; Fryxell, 1997). In the present study, Abelmoschus manihot is positioned as closely related to the two representatives of Hibiscus. Pavonia strictiflora was formerly Goethea strictiflora until it was returned to the genus Pavonia by Fryxell (1999). In my analysis, this species is the sister taxon to Malvaviscus arboreus and is more derived than the other closely related species of Pavonia. Radyera farragei was segregated out of Hibiscus by Fryxell and Hashmi (1971). My cladistic results may add some amount of support to this separation in that Radyera does not form a clade with Hibiscus, but rather it appears to diverge earlier from the tree. In the molecular analyses by Seelanan, Schnabel, and Wendel (1997) the phylogenetic position of Cienfuegosia was ambiguous in the Gossypieae clade. My trees indicate that Cienfuegosia ulmifolia branches off prior to Thespesia populnea and Gossypium hirsutum in the clade.

In the current study, a large volume of ontogenetic and morphological data has been accumulated from a representative sampling of the Malvaceae. There are, however, limitations to this study; one is that all the
genera in this large family could not be sampled. Another limitation is that some characters deemed useful for distinguishing members of the core Malvales by other researchers have not been included in the scope of the current research. Some of these possible synapomorphies, which may be important at various taxonomic levels, include: androecial vascular characters (Rao, 1952), anatomical features (Cronquist, 1968, 1988; Judd and Manchester, 1997), chemical characters (Cronquist, 1968, 1988; Judd and Manchester, 1997), ovule orientation (Bates, 1968; Judd and Manchester, 1997), embryo morphology (Fryxell, 1968; Judd and Manchester, 1997), trichome types (Bates, 1969; Fryxell, 1988; Judd and Manchester, 1997), whether flowers are unisexual or bisexual (Judd and Manchester, 1997; Bayer et al., 1999), leaf blade complexity (Bates and Blanchard, 1970; Judd and Manchester, 1997), and more detailed pollen characters (Fryxell, 1968, 1975, 1988; Fryxell and Hashmi, 1971; Christensen, 1986; Judd and Manchester, 1997; Bayer et al., 1999). The presence of an endoglossum, an internal appendage dividing the carpel into cells, may also be useful taxonomically (Bates 1969; Dorr, 1990); though Fryxell (1988) cautions that the term has been applied to a variety of structures that may not be homologous. Most seed characters appear to be useful mainly at the species level (Fryxell, 1968; Bates, 1969), except possibly for one character: whether they are associated with elongated hairs in the fruit (Judd and Manchester, 1997). Recently, chromosome numbers have been used to separate groups in the Malvaceae and in the order (Bates, 1968, 1969, 1976; Bates and Blanchard, 1970; Fryxell, 1968, 1988; Fryxell and Stelly, 1993). Disadvantages to using chromosome numbers include the fact that chromosome counts have not been made for many
Malvalean taxa, many inaccurate counts have been reported in the literature, and that delimitation of character states is problematic.

The present research demonstrates that ontogenetic data in addition to various types of morphological data can help to elucidate phylogeny in the Malvavisciae. Based on this preliminary analysis, three of the currently recognized tribes are tentatively supported. The Hibisceae is not clearly delineated and the monogeneric tribe Decaschistieae was not examined. Hopefully, larger analyses with more taxa and more characters will help to increase our understanding of the natural groupings within the Malvaceae s. str. and further our knowledge about phylogeny within the Malvaceae and its sister families.

LITERATURE CITED


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Gentry, A. H. 1993. A field guide to the families and genera of woody plants of Northwest South America (Colombia, Ecuador, Peru) with supplementary notes on herbaceous taxa. Conservation International, Washington, DC.


Moncur, M. W. 1988. Floral development of tropical and subtropical fruit and nut species. CSIRO Natural Resources Series No. 8, Melbourne.


CHAPTER 7
SUMMARY OF MALVACEAE PROJECT

SYNOPSIS OF RESEARCH

This study was designed to examine floral ontogeny in the plant family Malvaceae. Goals of this research include clarifying several aspects of floral development (i.e. answering certain morphological questions), comparing floral development among the tribes and among selected genera, using ontogenetic characters to characterize the tribes and the family, and adding insight into phylogenetic relationships within the family.

To achieve the goals of this research, material of selected species in each of the tribes of Malvaceae (excluding Decaschistieae which is monotypic) was obtained. For this project, Malvavisceae was represented by six taxa, Hibisceae by four taxa, Gossypieae by three taxa, and Malveae by eight taxa. In addition, material was also collected from representatives of the closely allied families Sterculiaceae and Bombacaceae. FAA-ethanol preserved floral material was examined using scanning electron microscopy (SEM) techniques (Chs. 2 - 5). Essentially complete ontogenetic series were obtained for most representatives. Examination of herbarium material with light microscopes and a survey of the literature were also used to complete mature floral and vegetative descriptions (Chs. 2 - 5). Information obtained about floral ontogeny in the above mentioned 24 taxa, in addition to two other taxa, was converted to discrete characters and combined with various types of morphological data in a cladistic analysis of the Malvaceae (Ch. 6). A list of species examined this research is provided in Table 7.1.

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TABLE 7.1. List of Malvalean taxa examined in this research and the chapters or references where ontogenetic floral descriptions and scanning electron micrographs are provided. Voucher information and additional literature citations are available in the chapters listed below and in Chapter 6.

<table>
<thead>
<tr>
<th>Taxon</th>
<th>Chapter or reference</th>
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<tr>
<td><strong>Malvaceae</strong></td>
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<tr>
<td>Malvavisceae</td>
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<tr>
<td><em>Malachra capitata</em></td>
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<tr>
<td><em>Malvaviscus arboreus</em> var. drummondii</td>
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<tr>
<td><em>Pavonia bahamensis</em></td>
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<tr>
<td><em>Pavonia spinifex</em></td>
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<tr>
<td><em>Pavonia strictiflora</em> (=Goethea strictiflora)</td>
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<td><em>Urena lobata</em></td>
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<tr>
<td><strong>Hibisceae</strong></td>
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<td><em>Abelmoschus manihot</em></td>
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<tr>
<td><em>Hibiscus acutosepalus</em></td>
<td>(Ault, 1987)</td>
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<td><em>Hibiscus lasiocarpos</em></td>
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<tr>
<td><em>Kosteletzkya virginica</em></td>
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<td><em>Radyera farragei</em></td>
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<tr>
<td><strong>Gossypieae</strong></td>
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<td><em>Cienfuegosia ulmifolia</em></td>
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<tr>
<td><em>Gossypium hirsutum</em> var. DPL50</td>
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<tr>
<td><em>Thespesia populnea</em></td>
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<td><strong>Malvaeae</strong></td>
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<td><em>Abutilon parishii</em></td>
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<tr>
<td><em>Anisodontea x hypomandarum</em></td>
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<td><em>Callirhoe involucrata</em> var. involucrata</td>
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<tr>
<td><em>Iliamnaremonta</em></td>
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<td><em>Lavatera trimestris</em></td>
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<td><em>Malva neglecta</em></td>
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<td><em>Modiola caroliniana</em></td>
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<td><em>Sida rhombifolia</em></td>
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<tr>
<td><em>Sterculia ceramica</em></td>
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<tr>
<td><em>Theobroma cacao</em></td>
<td>(Moncur, 1988; Bayer and Hoppe, 1990)</td>
</tr>
<tr>
<td><strong>Bombacaceae</strong></td>
<td></td>
</tr>
<tr>
<td><em>Pachira aquatica</em></td>
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</table>
Clarification of various aspects of floral development -- The association between the corolla and the androecium -- The nature of the association between petals and stamens in members of Malvaceae is ambiguous in much of the previous literature. One controversial issue involves whether during some stage of development a petal-stamen ring meristem forms (Payer, 1857; Gore, 1935; van Heel, 1966; Moncur, 1981; Ault, 1987) or not (Sattler, 1973). I found that petal-stamen ring meristems initiate in all members of Malvaceae examined in this study. In these taxa, the adnation of petals to the androecium is achieved in part by congenital fusion (the shared ring meristem), and in part by intercalary growth below the area of attachment.

Another dispute centers around whether common petal-stamen primordia are present in Malvaceae. Most previous researchers did not describe any common petal-stamen primordia in members of the Malvaceae, but they did depict common androecial mounds in some taxa (Payer, 1857; Gore, 1935; Sattler, 1973; Ault, 1987). Presence of common petal-stamen primordia in some malvaceous taxa was alluded to by van Heel (1966). In the present research, common petal-stamen primordia or mounds initiate in flowers of Malvavisceae, Hibisceae, Gossypieae, and most Malveae, although in some taxa it is difficult to ascertain (e.g. Callirhoe involucrata). Lavatera trimestris and Anisodontea X hypomandarum appear to lack common petal-stamen mounds.

The literature is contradictory as to whether the petals or the stamens initiate first in Malvaceae. Petal initiation has been described as preceding stamen initiation (Payer, 1857; Moncur, 1981; Ault, 1987), as supposedly following stamens (Duchartre, 1845), or as appearing at more or less the
same time as the first androecial primordia (Gore, 1935; Sattler, 1973). Van Heel (1966) concluded that in Ureneae (now Malvavisceae) and Hibisceae (which then included members of the Gossypieae) the petals seem to arise before any stamen primordia, but in Malveae the petals arise when some of the stamen primordia are present. I found that the petal primordia initiate concurrently or nearly so with the first common stamen primordia (or first staminal partitioning event) in all the representatives of Malvavisceae, Hibisceae, and Gossypieae; but in most Malveae petal initiation is delayed until after stamen proliferation is well under way.

In most representatives of Malvaceae in the current study, the stamen groups are opposite or nearly opposite the petals, but there are several exceptions. In *Sida rhombifolia*, an early stage of development shows ten common stamen primordia in the first set, but rather than the typical situation of an associated pair of these common stamen primordia positioned on the same radius as each petal, in *S. rhombifolia* only one of the associated pair is on the petal radius, while the other is alternate. In the early stages of androecial development of *Modiola caroliniana* and *Malachra capitata*, only five common stamen mounds appear in the first set and these are positioned alternate to the petals.

Timing varies among taxa as to steps in stamen initiation. According to my research, there are several scenarios for early formation of the petal-stamen complexes. In the first scenario, a petal-stamen ring meristem forms first; then five large mounded areas develop on the ring meristem. At the base of each mound, a petal initiates and the raised portion becomes partitioned into common stamen primordia. With this scenario, there is no problem in labeling the initial raised rim as a petal-stamen ring meristem.
since both organ types initiate on it. In most cases, five mounds easily fit into the definition of common petal-stamen mounds or meristematic regions since they give rise to both organs. Both organ types initiate on the mounded regions or at least initiate in the vicinity of the original mounds if the latter become less distinct with ring meristem enlargement. This type of initiation was found in most of the representatives of the Malvaviscæae and Hibisceæae. A variation of this is found in *Abutilon parishii*, in which a ring meristem forms first, after which the petal primordia and five large common staminal mounds appear concurrently. It is not known if common petal-stamen mounds develop between these events.

Another scenario involves the formation of the ring meristem concurrently with the five common mounded areas. Again, the terminology of petal-stamen ring meristem and common petal-stamen mounds would apply because of the fate of these structures. This type of development was found in *Malva neglecta*, *Sida rhombifolia*, and *Cienfuegosia ulmifolia*.

With the third scenario, first a petal-stamen ring meristem forms. Then the apical portion of the meristem becomes partitioned into ten common stamen mounds with petal primordia initiating basally on the ring meristem during some stage of androecial partitioning. No stage with five common petal-stamen mounds or five common stamen mounds develops. This type of development is takes place in *Anisodontea x hypomandarum*, *Lavatera trimestris*, and possibly in *Abelmoschus manihot*.

A fourth scenario has the five common mounded areas initiating first and then the formation of a raised peripheral rim and the central depression. The five common mounds may or may not be well defined and may or may not persist with formation of the ring structure. Since the five common
mounded areas give rise to a structure that ultimately will produce both petals and stamens, the term common petal-stamen mounds or meristematic regions can be applied. The mounded ring structure that ensues produces both petals and stamens, and thus can be characterized as a petal-stamen ring meristem. This type of development with mounded areas forming before the petal-stamen ring meristem was found in *Lliamna remota* and *Gossypium hirsutum*.

Determination of the order of development of the early petal-stamen complexes in some species is complicated. In some taxa the early ring meristem or the five common mounds are poorly defined and both develop very quickly. In *Hibiscus lasiocarpos* the five common petal-stamen mounds are so poorly defined and persist for such a short time that they can easily be missed. Often there are gradations between these types of initiation. For example, in *Urena lobata* and *Radyera farragei*, it is difficult to ascertain if they follow the first or the second scenario.

Differences between my interpretations and those of earlier researchers may be due to taxon differences, or to the use of different techniques, which do not give the same resolution as SEM. According to Ronse Decraene, Clinckemaille, and Smets (1993) observation of common petal-stamen complexes can be very difficult and critical stages are often missed because the primordia divide rapidly and the petals sometimes develop very slowly. Since petal development is delayed in Malvaceae, the use of primordial size is not a reliable way to determine the sequence of inception of petals and stamens. In addition, some of the conflict over the sequence of inception may be due to confusion in distinguishing common petal-stamen mounds from common androecial mounds. Difficulty in
observation of common petal-stamen mounds is compounded in some Malvaceae by the fact that after initiation, the mounds may become less defined with enlargement of the ring meristem as in *Hibiscus lasiocarpos* and *Radyera farragei*. In some cases, the mounds are either apparent for such a short time that the critical stage are easily missed or they are too poorly defined to be diagnosed with any certainty, as in *Abelmoschus manihot* and *Gossypium hirsutum*.

Clearly there is a strong developmental association between the corolla and the androecium in members of the Malvaceae. Both organ types initiate from a common floral meristematic structure, and this structure is a petal-stamen ring meristem. The common petal-stamen meristematic mounds can be considered as variations of the topography of the portion of the floral apex designated to form the petal-stamen ring meristem. Depending on the taxon, these common mounds may occur at any time during the formation of the petal-stamen ring meristem or may be absent. In some taxa, these common mounds result in the first partitioning of the ring meristem into sectorial regions. The fact that there are several different pathways to formation of the petal-stamen ring meristem and many gradations between these pathways, illustrates the plasticity of the petal-stamen ring meristem in Malvaceae.

**Stamen proliferation** — Another developmental objective of this research was to examine the modes of stamen proliferation in different members of the Malvaceae and to see if there is a link between different initiation patterns and anther divergence from the staminal column. The anthers reportedly can diverge singly, in pairs, or in more complex patterns (van Heel, 1966).
All of the representatives that I studied in Malvaceae have a single whorl of stamens in the androecium. Depending on the species, this whorl may consist of one set or many sets of stamens. The designation of a whorl in this case is based on the premise that all of the stamens or sets of stamens that make up the whorl originated from five common mounds, five common primordia, and/or a ring meristem. I did not observe a second whorl of androecial members initiating independently of the first whorl. Some previous investigators (e.g. Payer, 1857; van Heel, 1966) used the terms series and whorl interchangeably for structures that I call sets within a whorl, making direct comparisons difficult.

Multistamenesy is common in Malvaceae and several factors are responsible for this condition (Chs. 2 - 4). First of all, there is the formation of an androecial ring meristem. Endress (1994) stated that in flowers with a ring-like androecial mound, initiation of the gynoecium before the individual stamens or at least before the last stamens (as in Malvaceae) allows the floral apex to expand, so that the androecial part of the floral apex is separated from the gynoecial part by a furrow and proliferates in the form of a ring-mound. Many other angiosperms give rise to many stamens from ring meristems (Ronse Decraene and Smets, 1991, 1992; Endress, 1994).

Another factor that contributes to the large numbers of stamens in Malvaceae is the partitioning of the ring meristem into many common stamen primordia, i.e. the initiation of common stamen primordia and/or stamen primordia in each mounded area or sectorial region on the ring meristem. Generally, partitioning occurs in sets of five or multiples of five common stamen primordia, with simultaneous initiation within each set (Chs. 2 - 4). This process of proliferation is also referred to as complex or secondary
polyandry (Ronse Decraene and Smets, 1987, 1992; Endress, 1994) and has been reported in many plant families (Ronse Decraene and Smets, 1987, 1992; Bayer and Hoppe, 1990; Endress, 1994). The direction of androecial partitioning is lateral and centrifugal in most Malvaceae, but some Malvaviscaceae also partition centripetally. The early pattern of androecial partitioning varies depending on the species (Chs. 2 - 4).

Furcation of common stamen primordia also contributes to large stamen numbers. Furcation of common primordia is the actual splitting of primordia. It differs from partitioning events, i.e. the progressive utilization of virgin space by initiation of primordia or common primordia from a common meristemmatic region, common mounds, or ring meristems. Typically, representatives of Malvaceae have common stamen primordia that bifurcate, i.e. divide into two equal stamen primordia. Some extra large common multistamen primordia that trifurcate or quadrifurcate occur in  

\textit{Lliamna remota} and \textit{Gossypium hirsutum}, cotton (Chs. 2 - 4). Primordia which divide several times have been reported in cotton by Gore (1935) and in \textit{Alcea rosea} by Sattler (1973); although it is unclear whether the multiple divisions they refer to occur sequentially or synchronously.

Previous researchers (Payer, 1857; Saunders, 1936; van Heel, 1966) have attempted to attribute the formation of bisporangiate anthers or “half-anthers” in some Malvales to the bifurcation or serial splitting of common stamen primordia. If bifurcation were the cause of reduction in sporangia number from four to two per anther in members of Malvaceae, then one might assume that each common primordium should divide once, and only once. Otherwise we might obtain anthers that are unisporangiate or tetrasporangiate. In the current research, however, bisporangiate anthers
result from staminal members that have not undergone any furcation; this is especially common for the last-formed androecial members in some taxa. They may also result from primordia that divide several times without change in the sporangia number (Payer, 1857; Gore, 1935; van Heel, 1966; Sattler, 1973). I found that the large common multistamen primordia of *Iliamna remota* and *Gossypium hirsutum* that trifurcate or quadrifurcate produce bisporangiate, not unisporangiate, anthers. In addition, if the bisporangiate condition was the result of bifurcation, one would expect to always have an even number of stamens; this is not always the case. For example *Malvaviscus arboreus* typically has 25 stamens, all with bisporangiate anthers. This odd number results from the last five staminal primordia not bifurcating (Chs. 2-4). Further evidence that bifurcation is not solely responsible for the bisporangiate condition is found in Sterculiaceae and Bombacaceae. In *Theobroma cacao* (Sterculiaceae) members of only one of the two stamen whorls bifurcate, yet both whorls produce tetrasporangiate anthers (Bayer and Hoppe, 1990; Ronse Decraene and Smets, 1993). I found a similar situation in *Herrania sp.* in which only some primordia of the outer stamen whorl bifurcate, yet all the anthers in this whorl are tetrasporangiate. In *Adansonia digitata* and *Quararibea guianensis* (Bombacaceae) all the stamens initiate as discrete primordia that “do not divide into two halves” (no bifurcation), yet all of the anthers are bisporangiate (van Heel, 1966). Therefore, bifurcation does not correlate with the bisporangiate condition.

Saunders (1936) hypothesized that an early division in the androecium establishes the bisporangiate condition in Malvaceae. The earliest divisions of the androecium usually involves partitioning of the
common stamen mounds or sectorial regions on the ring meristem. In most malvaceous taxa examined in the present research the first five common mounds are partitioned laterally into two primordia; but in some species, like *Thespesia populnea*, the first five common mounds are each partitioned laterally into three primordia. In *Malachra capitata*, the first five common stamen mounds undergo bifurcation without first partitioning. So the earliest division of an androecial region can involve partitioning into two common primordia, partitioning into several common primordia simultaneously, or be a bifurcation event; yet all these result in an androecium with bisporangiate anthers. In *Sterculia ceramica* (Sterculiaceae) anthers are tetrasporangiate regardless of whether primordia are discretely initiated or result from partitioning. So tetrasporangiate anthers develop even if bifurcation and partitioning occur in the Sterculiaceae, and bisporangiate anthers develop in the Bombacaceae and Malvaceae regardless of whether bifurcation or partitioning occur (Chs. 2-5). Further proof comes from *Ricinus* (Euphorbiaceae) in that the process of splitting is described as "repeated ad infinitum" (Ronse Decraene and Smets, 1993). Therefore, bifurcation and partitioning are simply two means of stamen proliferation and do not determine sporangia number.

The degree of stamen filament connation varies considerably in members of Malvaceae. Filaments may diverge from the mature androecial column singly, in pairs, in partially fused pairs, or in small variously fused groups. Basal connation of the filaments above the point of attachment to the androecial tube may be attributed to several factors (Chs. 2-4). First, there can be exaggerated elongation of the base or stalk supporting a peanut-shaped common primordium prior to bifurcation. Secondly, the bifurcation...
may affect just the apical portion of the common primordium, leaving a common zone below. Lastly, after bifurcation, elongation of the filaments can occur mostly above or below the point of common divergence. If elongation occurs above this point, the filaments may appear distinct but very close together on the androecial column. The closeness of these paired filaments depends on what part of the androecial column elongates. Elongation of the androecial tube below where the filaments diverge results in the filaments remaining close together, whereas elongation of the tube at the level of filament divergence results in a less obvious association between the paired filaments. If elongation of the filaments occurs below the point of common attachment or by one of the other methods described, then the filaments appear fused to some extent. Partially fused filaments between stamen pairs have also been reported in Malvaceae by Ault (1987) and van Heel (1966, 1969) and in other plant families by Davis and Mariamma (1965) and Ronse Decraene and Smets (1993).

**Development of sterile androecial teeth** -- A third morphological objective was to study the development, or lack of development, of sterile teeth in Malvaceae. Four of the tribes of Malvaceae have sterile teeth at the apex of the staminal column, whereas the Malveae lack sterile teeth (Fryxell, 1988). I studied how the androecial teeth develop and whether some of the taxa that lack teeth at maturity actually initiate the primordia but then undergo suppression.

The literature is contradictory about the position of the sterile teeth as alternate to or opposite the petals. According to Saunders (1936), the sterile teeth are opposite the petals and thus are the termination of the five fertile antepetalous members, and not an aborted sterile antesepalous stamen
whorl as suggested by previous investigators. Payer (1857) and van Heel (1966) both reported that in some taxa, the sterile teeth are alternate to the petal radii, and in other taxa they are opposite the petal radii. My results are similar to Payer's and van Heel's in this matter. I found that in most cases, the sterile teeth are more or less in line with the stamen groups which are usually opposite the petal radii, i.e. one sterile tooth originates from the interior surface of each common petal-stamen region. There are, however, some exceptions to this. Three members of the Malvavisciaeae have androecial teeth that do not appear to be in line with the stamen groups. One of these, *Malachra capitata*, has the stamen groups alternate to the petal radii; thus the sterile teeth are still opposite the petal radii. The other two taxa, *Pavonia strictiflora* and *Urena lobata*, have sterile teeth that are alternate to the petal radii. In *Thespesia populnea* (Gossypioeae) the teeth are in line with the stamen groups, but the stamen groups are on radii alternate to the petals, and so the sterile teeth are also alternate to the petal radii. *Lavatera trimestris*, a member of the Malveae with androecial teeth suppression, initiates teeth alternate to the stamen groups and to the petal radii. Therefore, based on the results of this research, the sterile androecial teeth may be alternate or opposite with regard to the stamen groups and/or the petals. Several factors make the position of the androecial teeth sometimes difficult to determine. First of all, by the time the teeth initiate, the androecial column has started to elongate, the distinction between stamen groups is less clear with crowding of the stamen primordia, and the petals have broadened and may even overlap. In addition, the sterile teeth usually do not initiate exactly on the radii of the stamen groups; they often initiate off-median where there is space remaining in front of the lagging stamen rows.
In the tribes that typically have sterile androecial teeth, most taxa have five small spaces (areas of meristematic tissue not incorporated into staminal primordia) present on the inner apical surface of the petal-stamen ring meristem during early androecial partitioning events. These small spaces often elongate and contribute, at least in part, to the sterile teeth; but the teeth can form even if these spaces are absent. In the Malveae, *Malva neglecta*, *Sida rhombifolia*, and *Modiola caroliniana* have these small spaces on the young androecial ring meristem, but as the ring meristem elongates into a tube, this tissue does not develop into teeth but rather seems to be incorporated into the stamens. Therefore, having the extra meristematic spaces on the ring meristem does not necessarily dictate that the teeth will form (Chs. 2 - 4).

Sterile androecial teeth can develop even when space is not present on the inner apical surface of the young androecial ring meristem. In this situation the teeth appear to develop from tissue on the interior vertical surface of the ring meristem as it elongates into a tube; examples include *Pavonia strictiflora*, *Radyera farragei*, *Gossypium hirsutum*, and *Thespesia populnea*. In *Callirhoe involucrata*, *Lavatera trimestris*, and *Anisodontea x hypomandarum* (all in Malveae) minute to small sterile teeth develop in this way during early elongation of the short androecial tube into a column, but these teeth fail to develop fully and are completely absent at anthesis.

As previously mentioned, three representatives of the Malveae initiate but then suppress sterile teeth, whereas five representatives have no external evidence of sterile teeth initiation. I examined several different aspects of androecial tube development to determine if any could account for the lack of mature sterile teeth in the some Malveae. The shape of the petal-
stamen ring meristem is circular to pentagonal and the petals are typically alternate to the sepals in all taxa, regardless of whether the teeth form. Merosity of stamens is not a factor since teeth are present in taxa that have low to high stamen numbers, and are absent in taxa with the same range of stamen numbers. There does not appear to be any correlation between the presence or absence of sterile teeth and whether the first set of common stamen primordia contains five, ten, or more members; whether the stamen groups are in line with or alternate to the petal radii; whether the androecial column is exserted or included; the overall height of the androecial column; or the pattern (scenario) of ring meristem formation. Based on casual observation, there does not appear to be any correlation between the presence or absence of sterile teeth and the size (total diameter and inside diameter) of the ring meristems at various stages. Elongation of the androecial tube occurs throughout partitioning events, during furcation of common stamen primordia, and during the process of stamen differentiation; there are not any noticeable delays or accelerations in elongation at various stages between taxa with sterile teeth and those without.

This SEM study was able to exclude several factors as possibly accounting for presence or absence of sterile androecial teeth, but the exact mechanism behind the formation of sterile teeth is still elusive. In addition, this research has shown that sterile androecial teeth are initiated but suppressed in some members of Malveae. To resolve the homology of the sterile teeth in Malvaceae more research employing ontogenetic, anatomical, and genetic techniques is needed.

Carpel initiation -- Carpel development varies among malvaceous genera as to whether they initiate as one discrete whorl, as two whorls, or as
randomly scattered carpels (Payer, 1857; Bates, 1968; van Heel, 1978). In addition, there is controversy about whether a ring meristem is (Gore, 1935; Sattler, 1973; Ault, 1987; van Heel, 1995) or is not (Payer, 1857; Sattler, 1973; van Heel, 1978) involved in carpel initiation of some taxa. Also, certain members of the Malveae (former Malopeae taxa) have been described with (Payer, 1857; Endress, 1981) and without (van Heel, 1995) common carpel primordia. An unusual characteristic of the Malvavisceae is a gynoecium consisting of ten styles and stigmas but only a five-locular ovary. In members of this tribe ten carpels initiate in two sets (or whorls); one set is fertile and one is sterile. Opinions vary as to whether both sets are in the same spatial whorl, whether the first or the second set is fertile, and position of the carpel sets relative to the petals (Payer, 1857; Baillon, 1875; Saunders, 1936; van Heel, 1978). To clarify some of these aspects of carpel ontogeny, selected members of the Malvaceae were examined in this research.

Only one whorl of carpels initiates in representatives of Hibisceae, Gossypieae, and Malveae, although the aberrant collection of *Abelmoschus manihot* may be an exception. The carpels are arranged in a single spatial whorl (i.e. all are equidistant from the center of the axis) and the order of initiation is simultaneous. In members of the Malvavisceae, the gynoecium initiates as two consecutive sets of carpel primordia, or in this case two whorls. Rather than an inner and outer whorl, both sets of carpels are equidistant from the central axis and thus share the same spatial whorl. Each set or whorl contains five simultaneously initiated carpel primordia. In representatives of all the tribes, a small apical residuum remains in the center of the young gynoecial whorl (Chs. 2 - 4).
Carpel ring meristems appear to be lacking in the Hibisceae and Malvavisceae, but are present in the Gossypieae and Malveae. In a few representatives of the aforementioned tribes, this character could not be ascertained. Determination of a carpel ring meristem in this family is difficult for several reasons. First, when a ring meristem is present at carpel initiation, it is often low and poorly defined. Secondly, the carpel primordia may initiate on the ring meristem without any obvious increase in size or definition of the ring meristem, which suggests that carpels form rapidly after the ring meristem and that critical stages showing formation of the ring meristem may be easily missed. Thirdly, some of the members of this family have such high carpel numbers that the carpel primordia may appear to be connate due to crowding. I found no evidence of common primordia in the taxa in this study, although it should be noted that members of the Malopeae were not included.

Position of the first set of carpels differs among taxa in the Malvavisceae. The first set of carpels consistently initiates alternately to the sterile teeth. However, because the position of the teeth (alternate or opposite in relation to the petals) varies among taxa, the position of the first set of carpels also varies among the taxa (alternate or opposite in relation to the petals). In Malvaviscus arboreus, Pavonia bahamensis, and Malachra capitata members of the first set of carpels are generally alternate to the petals. In Pavonia strictiflora and Urena lobata the first carpel set initiates opposite to the petals.

Members of Malvavisceae also differ as to which carpels are fertile. In Urena lobata, the first set of carpels is fertile. In all other representatives where the course of carpel initiation is known, the second set of carpels
is fertile. The development of the sterile carpel bases is limited to different
degrees, according to the species. None of the sterile carpels form functional
locules, but some form small crevices (*Pavonia strictiflora* and *U. lobata*) or
dimples (*Pavonia spinifex*). The side walls of the fertile locules in the three
species of *Pavonia* appear to be joint products of both the sterile and the
fertile carpels. In *Malvaviscus arboreus* and *Malachra capitata* the sterile
carpels seem to be primarily responsible for the lateral walls of the locules;
this is due to the inward growth of the young sterile carpel bases. Only in *U.
lobata* are the locular walls primarily formed by fertile carpels.

**Bractlet homology and initiation** -- Although not one of the original
objectives of this project, during the course of this research it became clear
that little attention had been given to bractlet initiation by previous
researchers. Payer (1857) did not distinguish between floral bracts and
involucellar bracts or bractlets; he treated them both as homologous to
leaves and stipules. I found that involucellar bracts or bractlets are dissimilar
to leaves and floral bracts in several ways. Bractlets initiate on the floral
apex, whereas floral bracts and leaves initiate adjacent to the floral apex (i.e.
they initiate from the terminal branch apical meristem). It follows then, that
the bractlets initiate after the floral apex is formed rather than at the same
time or prior to the floral apex. In addition, several to many bractlets develop
with each flower, but typically only one leaf or floral bract subtends each
axillary flower or cluster of flowers. Therefore, in this respect the bractlets are
more likely homologous to the sepals than the floral bracts (Chs. 2 -4). The
issue then becomes whether the bractlets in malvaceous flowers can be
considered a second set of sepals. It is not unusual for flowers to have extra
whorls of organs, such as stamens (Cheung and Sattler, 1967; Tucker,
1987), sepals (Cheung and Sattler, 1967), and petals (Ramírez-Domenech and Tucker, 1990; Karrer, 1991; Ramírez-Domenech and Tucker, 1991; Lehmann and Sattler, 1993). There are, however, several reasons why the bractlets in Malvaceae should not be considered extra sepals. First, the bractlets and sepals within a single flower do not necessarily have the same morphological attributes or functions. Second, the bractlets and sepals in the same flower can arise by different initiation patterns (some helical, some simultaneous). Thirdly, the merosity of the bractlet and sepal whorls usually differ. A fourth reason is that the sepals are arranged in a whorl adjacent to the petals, but the position of the involucel can vary relative to the calyx. Most taxa examined in the current research have the involucel positioned in a whorl immediately adjacent to the calyx, but in *Anisodontea X hypomandarum*, *Callirhoe involucrata var. involucrata*, and *Thespesia populnea* and even in *Pachira aquatica* (Bombacaceae) some or all of the bractlets are spaced at various levels below the calyx (Chs. 2-5). Similarly, other researchers have reported that the bractlets in some malvaceous species have one or more bractlets spaced below the calyx (Bates, 1969; Fryxell, 1988; Dorr, 1990), inserted in a more or less irregular spiral arrangement (Fryxell, 1979), adnate to the calyx (Bates, 1969; Dorr, 1990), or even form a single monophyllous whorl with the calyx (Bates, 1969). Therefore, rather than considering the malvaceous bractlets as an extra sepal whorl, they should be considered as a distinctive type of floral organ.

The order of bractlet initiation and the presence of a bractlet ring meristem are both inconsistent in the previous literature (Payer, 1857; Sattler, 1973). In the present study, when involucels are present, initiation occurs in a helical sequence. *Radyera farragei* is unusual in having three helically
initiated common bractlet primordia, each subsequently partitioning into three bractlets. Presence of a bractlet ring meristem varies among taxa in the Malvavisceae and Hibisceae, but it is absent in the Gossypieae representatives studied. In the Malveae, only *Lavatera trimestris* has a bractlet ring meristem. The spatial separation of the involucel from the calyx in some taxa can be accounted for in part by the bractlet primordia initiating at slightly different levels on the floral apex and/or by subsequent elongation of the receptacle between the calyx and involucel.

**Comparison of floral development in the four major tribes of Malvaceae** — The major differences in floral ontogeny among the tribes in Malvaceae are summarized in Table 7.2. Detailed descriptions of floral ontogeny in particular species are available in chapters 2 - 4. The following characterization of the tribes is preliminary since only a limited number of taxa could be examined. It should be noted that Hibisceae and Malveae each contain a large number of genera and that there are genera in all four tribes that each contain numerous species. The provided summaries are compilations of ontogenetic and morphological data from this research project and may not necessarily reflect all features of the tribes. As more taxa are examined in each tribe the morphological and ontogenetic boundaries for each may have to be expanded and readjusted.

**Characterization of Malvavisceae** — Flowers in representatives of Malvavisceae generally have bractlets and when present the merosity ranges from three to twelve. The number of bractlets can be stable in some taxa or highly variable in others. In species that lack an involucel, a floral bract may subtend each flower. The sequence of initiation in the bractlet whorl is helical and the bractlets may be distinct or partially fused.
TABLE 7.2. Comparison of ontogenetic floral characteristics among four of the tribes in Malvaceae. Characterization is based on examination of the malvaceous taxa listed in Table 7.1, and will have to be modified as more taxa are investigated.

<table>
<thead>
<tr>
<th>Character</th>
<th>Malavisceae</th>
<th>Hibisceae</th>
<th>Gossypieae</th>
<th>Malveae</th>
</tr>
</thead>
<tbody>
<tr>
<td>Flower shape</td>
<td>tubular or open</td>
<td>open</td>
<td>open</td>
<td>open</td>
</tr>
<tr>
<td>Pedicel articulation</td>
<td>absent</td>
<td>absent or present</td>
<td>absent</td>
<td>absent or present</td>
</tr>
<tr>
<td>Number of bractlets</td>
<td>more than 3 or absent</td>
<td>more than 3 or absent</td>
<td>3 or may be suppressed</td>
<td>3 or absent</td>
</tr>
<tr>
<td>Relative bractlet position(^1)</td>
<td>adjacent</td>
<td>adjacent</td>
<td>adjacent or below</td>
<td>adjacent or below</td>
</tr>
<tr>
<td>Bractlet ring meristem</td>
<td>usually present</td>
<td>absent or present</td>
<td>absent</td>
<td>usually absent</td>
</tr>
<tr>
<td>Bractlet fusion</td>
<td>unfused or fused</td>
<td>unfused or fused</td>
<td>unfused</td>
<td>unfused or fused</td>
</tr>
<tr>
<td>Sepal initiation</td>
<td>helical or simultaneous</td>
<td>helical or simultaneous</td>
<td>helical</td>
<td>helical</td>
</tr>
<tr>
<td>Sepal ring meristem</td>
<td>usually present</td>
<td>usually present</td>
<td>present or absent</td>
<td>present or absent</td>
</tr>
<tr>
<td>Petal base appendages</td>
<td>none or auricles</td>
<td>none</td>
<td>ciliate tufts</td>
<td>ciliate tufts</td>
</tr>
<tr>
<td>Common petal-stamen mounds</td>
<td>present</td>
<td>present</td>
<td>present</td>
<td>present or absent</td>
</tr>
<tr>
<td>Relative timing of petal initiation(^2)</td>
<td>early</td>
<td>early</td>
<td>early</td>
<td>early or late</td>
</tr>
<tr>
<td>Number of stamens</td>
<td>10 to 50</td>
<td>~40 to &gt; 100</td>
<td>&gt;100</td>
<td>10 to &gt;100</td>
</tr>
<tr>
<td>Androecial exsertion(^3)</td>
<td>exserted or included</td>
<td>included</td>
<td>included</td>
<td>included</td>
</tr>
<tr>
<td>Stamen divergence from column</td>
<td>upper</td>
<td>throughout</td>
<td>throughout</td>
<td>upper or apical</td>
</tr>
</tbody>
</table>

(Table continued)
<table>
<thead>
<tr>
<th>Character</th>
<th>Malvaviceae</th>
<th>Hibisceae</th>
<th>Gossypieae</th>
<th>Malveae</th>
</tr>
</thead>
<tbody>
<tr>
<td>Androecial teeth</td>
<td>present</td>
<td>present</td>
<td>present</td>
<td>absent or suppressed</td>
</tr>
<tr>
<td>Initiation of androecium(^4)</td>
<td>scenario 1</td>
<td>scenarios 1</td>
<td>scenarios 1 or 2 or 3</td>
<td>scenarios 1 or 2 or 3 or 4</td>
</tr>
<tr>
<td>Directions of androecial partitioning</td>
<td>lateral, centrifugal, and/or centripetal; or no partitioning</td>
<td>lateral and centrifugal</td>
<td>lateral and centrifugal</td>
<td>lateral and centrifugal</td>
</tr>
<tr>
<td>Number of carpels</td>
<td>10</td>
<td>5(^*)</td>
<td>3-5</td>
<td>&gt;5</td>
</tr>
<tr>
<td>Number of carpel sets</td>
<td>2</td>
<td>1(^*)</td>
<td>1</td>
<td>1</td>
</tr>
<tr>
<td>Number of carpels that are fertile per gynoecium</td>
<td>half</td>
<td>all</td>
<td>all</td>
<td>all</td>
</tr>
<tr>
<td>Ovules per locule</td>
<td>1</td>
<td>1 or several or many</td>
<td>several</td>
<td>1 or several</td>
</tr>
<tr>
<td>Stigma type</td>
<td>capitate</td>
<td>capitate</td>
<td>capitate or decurrent</td>
<td>capitate or decurrent</td>
</tr>
<tr>
<td>Stylar fusion</td>
<td>partial</td>
<td>partial or complete</td>
<td>complete</td>
<td>partial</td>
</tr>
<tr>
<td>Carpel ring meristem</td>
<td>absent</td>
<td>absent</td>
<td>present</td>
<td>present or early connation</td>
</tr>
<tr>
<td>Fruit type</td>
<td>schizocarp or fleshy</td>
<td>capsule</td>
<td>capsule</td>
<td>schizocarp</td>
</tr>
<tr>
<td>Pollen shape</td>
<td>spheroidal</td>
<td>spheroidal or suboblate</td>
<td>spheroidal</td>
<td>spheroidal or suboblate</td>
</tr>
<tr>
<td>Pollen aperture type</td>
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<td>porate or colporate</td>
<td>porate or colporate</td>
<td>porate or colporate</td>
</tr>
</tbody>
</table>

(Table continued)
1. Position of bractlets with respect to the calyx: adjacent = bractlets are all in a whorl immediately subtending the calyx; below = one or more bractlets are positioned a distance below the calyx.
2. Timing of petal initiation relative to the androecium: early = petals initiate concurrent or nearly so with the first common stamen primordia; late = petals initiate after stamen proliferation is well underway.
3. Androecial exsertion: exserted = androecial column is taller than the corolla; included = androecial column is shorter than the corolla.
4. Early initiation of the androecium: scenario 1 = petal-stamen ring meristem then common petal-stamen mounds; scenario 2 = petal-stamen ring meristem concurrent with common petal-stamen mounds; scenario 3 = common petal-stamen mounds prior to the petal-stamen ring meristem; scenario 4 = petal-stamen ring meristem without common petal-stamen mounds. Further details about the scenarios for early initiation of the androecium are on available on pages 529-531.
* The atypical collection of Abelmoschus manihot has ten carpels (rather than five) and difference in size of the primordia may indicate that initiation occurs as two sets.
Calices are five-merous and the sepals are connate to some extent. Depending on the species, sepal initiation is either helical or simultaneous. A ring meristem precedes initiation of bractlets and sepals in some taxa, but not in others. A petal-stamen ring meristem precedes petal and stamen initiation. In each flower, five common petal-stamen mounds initiate on the shared ring meristem in positions that are alternate and interior to the sepals. From each of these common mounds a petal primordium initiates in an alternate or off-alternate position to the sepals, and concurrently a common stamen primordium initiates in a varying position relative to the position of the petals and sepals. Stamen proliferation progresses in a combination of lateral, centripetal, and/or centrifugal directions. Some of the stamen primordia initiate independently on the ring meristem (i.e. partitioning) and others result from bifurcation of common stamen primordia. Initiation within the petal whorl and within each of the sets of stamens is simultaneous. Each stamen group may be radially aligned or not with its associated petal (the petal that shared the same common petal-stamen primordia as the stamen group). The mature petals are distinct, adnate to the androecium, and in some taxa have auricles. Depending on the species, the corolla is either tubular or it flares distally to form an open flower. The androecial ring meristem elongates vertically and forms a column. At the top of the column, five sterile teeth form in variable position with regard to the petal positions. Filaments diverge from the column singly, or singly and in pairs. Stamen merosity is typically 50 or less and only in a few taxa are the stamens arranged in radial rows. In the gynoecium, ten carpel primordia initiate as two sets of five. The two sets or whorls of carpel primordia initiate alternately in the same spatial whorl. Initiation within each set of carpel primordia is
simultaneous. In most taxa, the second set of carpels is fertile and the first set is sterile. The sterile carpels may invaginate to varying degrees but do not form locules with ovules. The bases of the sterile carpels may or may not contribute to forming the sides of the fertile locules. Even though the bases of the sterile carpels become indistinct in the five-locular ovary, styles and stigmas develop on each of the ten carpel primordia. Pollen is typically spherical, polyporate, and spiny; the exception is *Pavonia strictiflora* with smooth grains. The fruit type is a fleshy or dry schizocarp with various types of surface coverings. Floral nectaries are present at the inner bases of the sepals.

**Characterization of Hibisceae** -- Representative flowers in the Hibisceae typically have four to fourteen bractlets that may be separate or basally fused. The number of bractlets varies among taxa and may vary within species. Bractlet primordia, or in the case of *Radyera* common bractlet primordia, initiate in helical sequence. Formation of a bractlet ring meristem may precede bractlet initiation in some taxa. The calyx is five-merous and basally fused. Initiation of the sepals may or may not involve a sepal ring meristem and the order of initiation can be simultaneous or helical. The corolla exceeds the calyx in length. The petals typically flare distally to form an open flower, but may in some species form a tubular corolla (Fryxell, 1988, 1997). The five petals are not connate but are basally adnate to the androecium. Prior to petal initiation, five common petal-stamen mounds are produced on a petal-stamen ring meristem. A petal primordium initiates on the outer perimeter of each mound at about the same time as a common stamen mound initiates on the raised surface. The order of initiation of the petals is simultaneous. The petals are positioned alternate to the sepals.
The androecium consist of 40 to 160 stamens; with numbers varying among taxa and within individual species. The first five common stamen mounds or regions become laterally divided to yield a whorl of ten common stamen primordia. From these ten common stamen primordia, proliferation of common stamen primordia proceeds in a centrifugal direction so that there are ten radial rows of common stamen primordia, usually five leading and five lagging radial rows. Most of the primordia in these rows will bifurcate in a lateral or oblique direction to yield two stamen primordia each. The stamen groups are basically opposite the petals. The filaments may diverge either singly or in pairs from the androecial column. Stamen filament divergence is radial and usually throughout the length of the column. At the apex of the androecial column, five sterile teeth are initiated. In some taxa the teeth may become lobed or divided at maturity. The pollen is spheroidal or rarely oblate to suboblate in shape, has numerous spines, and either porate or colporate apertures. The gynoecium is usually shorter than the corolla. It contains five fertile carpels (rarely 10 in aberrant collections). Each locule may contain one, several, or numerous ovules depending on the species. The ovary is syncarpous, superior, and has axile placentation. The styles are fused into a column that may diverge apically in some taxa. The stigma type is capitate and there is a one to one ratio of stigmas to mericarps. Early initiation of the gynoecium does not appear to involve a carpel ring meristem. All of the carpel primordia of the gynoecium initiate simultaneously in a single whorl (except in possibly aberrant polymerous flowers). There is an apical residuum in the center of the young gynoecium. The fruit type is a dehiscent capsule.
Characterization of Gossypieae -- Members of the Gossypieae usually have three bractlets, although in some taxa the bractlets may be suppressed to some degree. Fryxell (1979) listed most genera in this tribe with three bractlets, although some taxa may have none, or many. In the taxa I examined, bractlet ring meristems are not present and the order of bractlet initiation is helical. The bractlets remain distinct. In the five-merous calyx whorl the sequence of sepal initiation is helical. Petals initiate from common petal-stamen mounds on a petal-stamen ring meristem, but in some taxa the common mounds form prior to or concurrent with the ring meristem. The number of stamens ranges from 110 to 200, with variation among taxa and within a species. The first five common stamen mounds may divide laterally to form ten or 15 common stamen primordia. The common stamen primordia are generally arranged in ten radial rows, and there are usually sets of leading and lagging rows, but with some exceptions. Most of the stamen groups are opposite the petals, but in at least one taxon the stamen groups are alternate with the petals. The filaments diverge in pairs, in partially fused pairs, or singly. The pollen is typically spheroidal. The gynoecium consists of three to five fertile carpels with several ovules per locule. The styles are fused their entire length and may be terminated by capitate or decurrent stigma lobes. A low carpel ring meristem may be involved in carpel initiation. The fruit is a dehiscent or indehiscent capsule.

Characterization of Malveae -- In the Malveae, flowers of representative taxa typically have involucels, or less commonly lack them. When present, the bractlets are three to numerous and distinct; less frequently they are basally fused. In most cases, the involucl subtends the calyx, however some variation in position may occur. Bractlet primordia
initiate helically, usually without a bractlet ring meristem. The calyx is five-
merous, basally fused, and exceeds the involucel (when the latter is present) 
in length. Initiation of sepals is generally helical and may or may not involve 
a sepal ring meristem. The corolla exceeds the calyx in length and flares to 
form an open flower. The petals are not connate but are basally adnate to 
the androecium. The five petals initiate simultaneously at the base of a petal-
stamen ring meristem. Common petal-stamen mounds may develop prior to, 
during, or after formation of the petal-stamen ring meristem or they may not 
develop at all. Time of petal initiation may occur early with the first 
partitioning event of the upper androecial portion of the ring meristem or 
occur much later with the centrifugal proliferation of common stamen 
primordia. The petals are positioned alternate to the sepals. Petal 
elongation is delayed during stamen proliferation. The androecium consists 
of as few as five stamens to numerous (120 - 140) stamens, with numbers 
varying among and within species. The innermost set of common stamen 
primordia may contain five or ten members. After initiation of the first set of 
common stamen primordia, the proliferation of common stamen primordia 
progresses in a centrifugal direction. In taxa with large numbers of stamens, 
the common stamen primordia are arranged in radial rows, usually with 
leading and lagging radial rows. The innermost set or sets of common 
stamen primordia may bifurcate in a radial, oblique, or lateral direction. The 
common primordia in the outer sets bifurcate in a lateral to oblique direction. 
Some taxa may have large, common multistamen primordia which furcate to 
produce more than two stamen primordia. The stamens are produced in five 
regions or groups which are usually opposite the petals, although some 
exceptions are found. The filaments may diverge singly, in pairs, in partially
fused pairs, or in groups from the androecial column. Filament divergence is radial and may range from apical only to nearly throughout the length of the column. Although in some taxa sterile teeth may be initiated, at maturity the apex of the androecial column completely lacks sterile teeth. The pollen is spheroidal to spheroidal-suboblate in shape, is echinate, and has either porate or colporate apertures. The numbers of apertures appears to vary greatly among taxa; this is verified by actual counts made by Christensen (1986) and Fryxell (1988). The gynoecium is composed of six to numerous carpels, with the numbers varying among and within species. All of the carpels are fertile. Each locule may contain one to many ovules depending on the species. The ovary is syncarpous, superior, and has axile placentation. The styles are basally fused into a column and divergent apically. Stigmas are capitate or introrsely decurrent and there is a one-to-one ratio of stigmas to mericarps. The carpels initiate as a connate whorl and in some taxa may initiate on a carpel ring meristem. All of the carpel primordia of the gynoecium initiate simultaneously in a single spatial whorl (except perhaps in Malopeae). An apical residuum remains in the center of the young gynoecium. The fruit type is a schizocarp that may be indehiscent, dehiscent, or partially dehiscent. The fruits have obvious segmentation and are, with some exceptions, generally wider than tall with persistent sepals and bractlets. The surface of the fruits may contain a central disk, a variety of trichomes, and/or appendages such as lobes, spines, or caps.

**Floral ontogeny in Malvaceae** -- The following is a synopsis of malvaceous floral characteristics and ontogeny based on the results of research described in chapters 2 - 4 and the literature described therein.
These generalizations are based on examination of 21 malvaceous species and may need to be revised as more taxa are surveyed.

Members of the Malvaceae commonly have involucels. The number of bractlets may be three, four, five, or a variable number between four and fourteen (or more); or the involucel may be lacking. Bractlets initiate on the floral apex in helical sequence. A bractlet ring meristem may be present or absent depending on the species. In most taxa (with some exceptions), the bractlets are unfused, persistent, and positioned in a single spatial whorl directly below the calyx.

The calices in Malvaceae are five-merous and have trichomatous nectaries on the inner sepal bases. The sepals are connate to some extent, are valvate, and function primarily as protection in developing buds. In most taxa the calices are green. The species which have brightly-colored calices (Pavonia strictiflora and Malachra capitata) also have corollas, but the main attractant in these flowers appears to be either the bractlets or the floral bracts. The sepals typically initiate in helical order. There are some exceptions with simultaneous initiation, all of which have helically initiated involucels that precede the calices. A sepal ring meristem is present in most taxa, though it is often poorly defined.

The corolla is five-merous and may have a wide range of colors including white, cream, yellow, orange, pink, red, maroon, lavender, and even somewhat greenish. Basal color spots occur on petals in some taxa. Auricles or ciliate tufts of hair may be present or absent on the petal bases. The corolla typically exceeds the calyx in height, but in a few species it doesn’t exceed the involucel or floral bracts. The mature corolla usually flares to produce an open flower, but in a few taxa it forms a tubular flower.
In the bud, the petals are convolute. Timing of petal initiation typically overlaps with the early stages of initiation of the androecium. The petals initiate on a common petal-stamen ring meristem and often common petal-stamen mounds are involved. Initiation within the petal whorl is simultaneous. Petal elongation is generally delayed during proliferation of the androecium.

Stamen numbers vary from five to numerous in members of the Malvaceae. Usually, with a few exceptions, the androecium is shorter than the corolla. Stamens are fused basally into a column. The androecial column is adnate basally to the corolla. Filaments may diverge singly, in pairs, or in groups from the column; rarely the anthers are sessile. The anthers are bisporangiate and dehisce by longitudinal slits. Sterile androecial teeth may be present or absent at the apex of the column. The androecium consists of only one stamen whorl (at least in the taxa I have examined), but it may contain few to many sets of stamens that initiate in groups of five or multiples of five. Initiation within each stamen set is simultaneous. A petal-stamen ring meristem is present during some stage of development. There are, however, several ontogenetic pathways to the formation of this ring meristem; some of which involve the formation of common petal-stamen mounds prior to, concurrent with, or after ring meristem formation. In most taxa, especially those with high stamen merosity, the stamen primordia are arranged in more or less radial rows (usually ten rows) on the young androecial tubes. Stamen groups (sectorial regions) are generally in line with the petals. Proliferation of stamens generally occurs by partitioning and/or bifurcation in radial, lateral, or oblique directions.
Merosity of the carpels in Malvaceae varies from three to numerous. Carpel number may equal or double the fertile locule number. Depending on the taxon, one to numerous ovules develop in each fertile locule. The ovary is syncarpous and superior with axile placentation. The styles are partially or completely fused into a stylar column. Stigmas (or stigma lobes) are mostly capitate, but may be decurrent or less often wedge-shaped. The gynoecium is exserted (at least slightly) beyond the androecial column at maturity. Prior to or during initiation of the carpels, a low carpel ring meristem may be present or absent. Timing of initiation of the gynoecium usually overlaps with stamen proliferation. Members of the gynoecium may initiate as one or two sets in a single spatial whorl. The initiation sequence within each carpel set (or whorl) is simultaneous. Depending on the taxon, locule differentiation may occur in all or only some of the carpels. Typically, differentiation of ovules and sometimes of the stigmas begins prior to exsertion of the gynoecium beyond the androecium. An apical residuum is present interior to the young gynoecium.

The fruit type in Malvaceae is a capsule or schizocarp; rarely it is a fleshy schizocarp. The shape of the fruits varies, but in most of the representative taxa width exceeds height. The surface of the fruits may be smooth, rugose, lobed, hairy, or may bear various types of appendages such as spines, lobes, caps, barbs, or wings. The pollen is spheroidal (sometimes oblate to suboblate), polyporate or colporate, and is echinate (one exception is smooth).

Comparison of Malvaceae to Bombacaceae and Sterculiaceae — Malvaceae, Bombacaceae, and Sterculiaceae share many features such as valvate sepals, distinct petals, monadelphous or
polyadelphous filaments, multicellular glandular hairs localized on the sepals, and a variety of other floral and vegetative characteristics (Cronquist, 1981, 1988). A morphological floral character that separates the Sterculiaceae from the rest of the traditionally circumscribed Malvales is the combination of tetrasporangiate anthers and filaments fused into a tube (Gentry, 1993). Tetrasporangiate anthers are also found in Elaeocarpaceae and Tiliaceae, and a staminal tube in Bombacaceae and Malvaceae, but the combination is unique to Sterculiaceae. In addition, most Sterculiaceae have staminodes and reduced stamen numbers. Bombacaceae are differentiated from most other Malvalean families by a combination of character states: fused filaments (a feature shared by Malvaceae), being mostly arborescent (Malvaceae are mostly herbaceous or shrubby), and having pollen that is not spiny (Malvaceae has spiny pollen) (Gentry, 1993). These characters apply in general but there are some notable exceptions. For example, some Malvaceae (Wercklea, Thespesia, Hampea, Tetrasida, and some Hibiscus) are small trees (Ch. 3 and personal observations; Gentry, 1993) and at least one taxon (Pavonia strictiflora, formerly Goethea strictiflora) has smooth pollen (Ch. 2). Camptostemon in the Bombacaceae differs from the usual smooth or textured pollen in the family by having spiny pollen (van Heel, 1966). There is a similar wide range of stamen merosity in Sterculiaceae, Bombacaceae, and Malvaceae, but the overall distribution of stamen numbers varies among the families. This character may be useful at the tribal level in Malvaceae, but without surveying more taxa, its significance at the tribal level in Bombacaceae and Sterculiaceae is in question. Also, the distribution within the stamen merosity range may be helpful at the familial level. Another character that may be of use at the family level is the...
occurrence of sterile stamens in many Sterculiaceae, but not in Malvaceae (Chs. 2 - 4) or in Bombacaceae (van Heel, 1966). This, however, raises the question about whether the staminodes in Sterculiaceae are homologous with the sterile teeth and sterile apical collars found in some Malvaceae and Bombacaceae. Current classification does not use fruit type to delineate the families (although it has been used in the past); there are several fruit types in Sterculiaceae and Malvaceae and two types in Bombacaceae.

These families share several floral ontogenetic characteristics, based on results of the current research. One consistent feature is helical initiation in the outermost perianth whorl (bractlets or sepals) with a transition to simultaneous initiation of organ sets in the inner floral whorls (petals, stamens, carpels). This means that if sepals are the outermost whorl they initiate helically; but if a helically initiated involucel is present, the sepals may initiate helically or simultaneously. There is no evidence of bidirectional, unidirectional, or spiral (similar to helical but approaching or receding from the apex) initiation within the floral organ whorls. Helical initiation, however, of floral buds in an inflorescence or of floral bracts may occur. Other important shared characteristics include: partial or complete fusion of the calyx members; petals (when present) are not connate but are usually adnate to the androecium; and presence of some common stamen primordia (in flowers with more than five stamens) that partition and/or bifurcate. In addition, there is overlap in time of initiation of the gynoecia and proliferation of the androecia. In the taxa I examined, the carpels initiate as one or two sets in a single spatial whorl, have an apical residuum interior to the young gynoecium, and form a superior ovary.
One feature that is not consistent within the Malvaceae, nor perhaps in the other two families, is the presence of ring meristems in the involucels, calices, and gynoecia. Identification of ring meristems in these whorls is complicated because they are often poorly defined, are quickly overtaken by primordia and thus easily missed, and/or sometimes obscured by crowding of organ primordia at the time of initiation. Therefore, presence of a ring meristem is these whorls may not be the most reliable way to distinguish some taxa.

Several ontogenetic and developmental features of the androecium and gynoecium may be useful in delineating the families. In the Malvaceae only one stamen whorl initiates, whereas in the Sterculiaceae most reports describe two whorls. In the Bombacaceae (*Pachira aquatica*) I found two stamen whorls, but previous literature may indicate one or two whorls depending on taxon and investigating method used. In Malvaceae, an androecial ring meristem (in fact a petal-stamen ring meristem) develops. Based on my research and previous literature, an androecial ring meristem also appears to be common in the Bombacaceae, but not necessarily in the Sterculiaceae. In the Malvaceae there is an obvious enlargement of the ring meristem into a broad tube during stamen proliferation (Chs. 2 - 5). In Bombacaceae during stamen proliferation the androecium develops into a broad tube as in *Matisia* (Moncur, 1988), *Adansonia*, *Bombax*, and *Ochroma* (van Heel, 1966) or a cup-shaped structure as in *Pachira* (Ch. 5; van Heel, 1966). In contrast, the androecial area in Sterculiaceae tends to stay rather flat as in *Herrania sp.* (Ch. 5) and *Theobroma* (Bayer and Hoppe, 1990) or to develop into an androgynophore as in *Sterculia* (Ch. 5) during stamen proliferation. Although van Heel (1966) had few nonvascular illustrations of
Sterculiaceae to analyze, he stated that the mostly united basal part of the androecium develops fully only much later. Another possible difference is that usually in Malvaceae the stamen primordia are arranged in more or less radial rows (at least when high numbers of stamens are present) (Chs. 2 - 4). In the Bombacaceae, the stamen primordia may cover consecutively the entire androecial tube surface as in Adansonia (van Heel, 1966), be arranged in radial rows as in Bombax (van Heel, 1966) and Matisia (Moncur, 1988), or be arranged in clusters or fascicles as in Pachira (Ch. 5; van Heel, 1966). In Sterculia, the stamens appear to be arranged in groups on the androgynophore. The androgynophore is a feature that may be limited to the Sterculiaceae and absent in Malvaceae or Bombacaceae. In the Malvaceae and the Bombacaceae the gynoecium forms a syncarpous ovary and partly or completely fused styles, where as in the Sterculiaceae various degrees of syncarpy and apocarpy occur. Overall, the Bombacaceae appear to share more floral characteristics (both morphological and ontogenetic) with the Malvaceae than do the Sterculiaceae (Chs. 2 - 5). This judgment, however, is based on examination of only a few taxa in Sterculiaceae and Bombacaceae and on the very limited ontogenetic data available in previous literature.

Placement of certain taxa -- Another goal of this study was to lend some insight concerning the position of certain taxa. For a long time members of the Gossypieae were submerged in the Hibisceae (Maout and Decaisne, 1876; Schumann, 1891; Edlin, 1935; Kearney, 1951; Hutchinson, 1967), but the tribe Gossypieae was resurrected and redefined 1968 by Fryxell. Members of Gossypieae are unique to Malvaceae and angiosperms in having gossypol glands (Fryxell, 1968, 1975, 1979). Other characteristics
such as pollen structure (Fryxell, 1968; Christensen, 1986), embryo morphology (Fryxell, 1968), presence of involucral nectaries (Fryxell, 1968), and cytological data (Bates, 1965; Fryxell, 1968) also help to distinguish the members of Gossypieae from Hibisceae. Ontogenetically these two tribes are quite similar and they share several morphological attributes (Ch. 3, Table 7.2). At present, these two tribes should be considered as separate but closely allied.

Recently, the genus Goethea was incorporated in the large genus Pavonia (Fryxell, 1999). Malvaviscus arboreus shares more similar ontogenetic characteristics (including variable bractlet merosity, androecial teeth that are opposite the petals, and fertile carpels that are opposite or intermediate between opposite and alternate to petals) with Pavonia bahamensis and Pavonia spinifex than does Pavonia strictiflora (formerly Goethea strictiflora). P. strictiflora also differs from the other Pavonia species and Malvaviscus with regard to bractlet and sepal color and function. P. strictiflora shares several features with Urena lobata such as stable bractlet merosity, androecial teeth positioned alternate with the petals, and the first set of carpels opposite the petals (Ch. 2). Also, Goethea is unique in the family in having pollen without spines (Fryxell and Hashmi, 1971).

This information would seem to argue against Fryxell’s (1999) inclusion of Goethea strictiflora in Pavonia. Before realigning these genera or others, however, many more species of each genus need to be examined to determine how much ontogenetic variation there is within a genus. Pavonia is a rather large, diverse genus and with the examination of more taxa, the differences I found in P. strictiflora may well fall within the diversity of the genus.
Abelmoschus was separated from the genus Hibiscus on the basis of a calyx that is spathaceous, two- or three-lobed, and deciduous before the fruit matures (Kearney, 1951). Kearney (1951) also described earlier research by Skovsted (1944), who separated these genera based on hybridization studies, and a study by Hochreutiner (1924), which dismissed the character of a spathaceous calyx as being shared by certain species of Hibiscus. The latter author indicated that a good generic character is the "basal cohesion of the calyx with" the petal-stamen tube so that the calyx, petals, and stamens fall off as a unit. Fryxell (1988) also reported that species of Abelmoschus have a spathaceous calyx that splits asymmetrically at anthesis and falls off with the corolla. Although I lacked fully mature flowers of Abelmoschus manihot and cannot verify the amount of fusion or the caducous nature of the sepals, the early initiation of the calyx in this species was the same as in Hibiscus lasiocarpos. Both taxa initiate five sepals in a simultaneous order on a low sepal ring meristem and have connate sepals. In addition, I found no evidence of ontogenetic fusion of the calyx to the petal-stamen ring meristem or subsequent adnation between the calyx and the petal-stamen tube. In general, the early ontogeny of flowers in these two taxa is very similar. One character that does distinguish them is that in A. manihot the styles are fused their entire length whereas in H. lasiocarpos the styles separate apically. This may be considered a generic distinction since Fryxell (1988) characterized the genus Abelmoschus as having a single style with 5 sessile capitulate stigmas and the genus Hibiscus with five styles that are distally free with capitulate stigmas. Another distinction between these two taxa is that in H. lasiocarpos the pedicels are distinctly jointed, while in
A. manihot the pedicels are not jointed; it is unknown if this distinction can be applied to all members of these genera (Ch. 3).

Radyera has several features that set it apart from the other taxa in Hibisceae and justify its segregation from Hibiscus. According to Fryxell and Hashmi (1971), R. farragei is believed to be unique among the Malvaceae in having stipular nectaries; it is not known if this feature is also present in the other species of Radyera, R. urens. R. farragei is also unique in the Hibisceae in having both loculicidal and septicidal dehiscence, with the five-celled capsule dividing at maturity into ten segments; the Hibisceae typically has capsules with only loculicidal dehiscence (Fryxell and Hashmi, 1971). Radyera is also set apart from other malvaceous taxa (including Hibiscus) by some embryo characteristics, by having oblate to suboblate pollen grains that are zonicolporate with less than ten apertures. Current members of Hibiscus (and most of the Malvaceae) have spheroidal to spherical pollen that is panporate with many to numerous apertures. In fact, zonicolporate pollen has otherwise only been found in the Malveae. Radyera is also distinguished from Hibiscus by having an undivided style (this research; Fryxell and Hashmi, 1971). Other characters that I found in my examination of R. farragei that help to delineate the species (and possibly the genus) are the lack of jointed pedicels, connation of the involucellar bracts, absence of an involucellar ring meristem, helical initiation of common bractlet primordia, absence of a calyx ring meristem, helical initiation of the sepals, lack of space left on the androecial ring meristem in front of the lagging rows of stamens, and irregularity of the androecial teeth (Ch. 3). The combination of ontogenetic and morphological characters clearly separates Radyera from Hibiscus and may even place the genus at the periphery of the tribal limits.
Phylogeny in the Malvaceae -- Previous cladistic analyses using molecular (La Duke and Doebley, 1995; Ray, 1995; Seelanan, Schnabel, and Wendel, 1997; Alverson et al., 1998, 1999; Baum, Alverson, and Nyffeler, 1998; Bayer et al., 1999) or morphological data (Fryxell and La Duke, 1994; Judd and Manchester, 1997) are not in complete agreement about the delineation of the tribes. Therefore, an objective of this project was to test the monophyly of the tribes and examine the phylogeny in the Malvaceae using a combination of ontogenetic and morphological data. Another objective was to use the cladistic analysis to add insight into evolutionary relationships among the genera and to determine character evolutionary trends.

Phylogenetic trees produced in my analyses (Ch. 6) show that only three of the four commonly recognized tribes in Malvaceae s.s. are supported as discrete groups. Malvaceous taxa are divided into two large subgroups, one with members of the Malveae and the other consisting of the remaining three major tribes (excluding Decaschistieae). Members of the Malvavisceae form a clade and are part of a larger clade which includes members of the Hibisceae and ultimately the Gossypieae. Members of the Hibisceae are paraphyletic. Gossypieae and the Malveae are both monophyletic. Within the Malvavisceae clade, *Malvaviscus* and *Pavonia* are more highly evolved than *Malachra* and *Urena*. *Gossypium* and *Thespisia* are more closely allied than either is to *Cienfuegosia*. The relationship of taxa within the Malveae clade is unresolved. The bombacaceous taxon, *Pachira*, is more closely allied with the Malvaceae than the sterculiaceous representatives. In the resulting trees, Malvavisceae appears to be the most derived tribe and Malveae occupies a basal position in the family.
Bootstrap values for the aforementioned analysis are moderate to poor, but the results are similar to two previous analyses. La Duke and Doebley (1995) using molecular data and Fryxell and La Duke (1994) using morphological data described the division of the Malvaceae into two large groups with Malveae making up one of the groups. Similarly, they found that the Gossypieae and Malveae are each monophyletic and that Hibisceae is not monophyletic. Malvavisceae is also monophyletic according to Fryxell and La Duke (1994) but not according to La Duke and Doebley (1995).

Two analyses of the core Malvales, which included only a limited number of malvaceous taxa, have results somewhat contradictory to mine and the two aforementioned studies. Judd and Manchester (1997), using morphological data, described Gossypieae as most basal in the order and Hibisceae as the sister group to the Malveae + Malvavisceae. Both Malvavisceae and Malveae formed clades and were positioned as most advanced in the family. The molecular analysis by Alverson et al. (1999) depicted Malvaceae s.str. divided into two large clades, but with one consisting of Malveae + Gossypieae and the other of Malvavisceae + Hibisceae. In their consensus tree, only Gossypieae and Malvavisceae were monophyletic.

Several evolutionary trends are apparent in my cladistic analyses. Bractlet number tends to increase from zero (in the sterculaceous representatives) to three (in the bombacaceous taxon, the Gossypieae, and most Malveae) to mostly four or more (in Hibisceae + Malvavisceae). Bractlets have been lost in a few taxa. Primitive carpel number appears to be five with a progression to fewer in the Gossypieae clade and to more numerous in the Malvavisceae and Malveae lineages. Ovule number
exhibits an overall reduction pattern. Outgroup taxa, Gossypieae, and most of the Hibisceae have variable ovule numbers between two and many or even numerous per locule. The Malveae clade is diverse for this character with ovule numbers of one two, three, or variable. The Malvavisceae + Kosteletzkya possess one ovule per locule. Though not well defined, transitions occur in pollen apertures from colporate to porate and in pollen aperture number from three to variable (with numbers ranging from two to numerous). Schizocarpic fruits may have evolved twice in the Malvaceae, though this observation may be due to the somewhat ambiguous placement of the Hibisceae members. The early sequence of androecial initiation varies among taxa in this analysis. There appears to be a general phylogenetic trend in androecial development from: either not having a ring meristem or the initiation of common petal-stamen mounds prior to development of a ring meristem -> initiation of the ring meristem concurrent with common petal-stamen mounds or just initiation of the ring meristem without common mounds -> initiation of a ring meristem prior to initiation of common petal-stamen mounds. Stamen merosity is homoplasic, though the more recently derived taxa, Malvavisceae + Kosteletzkya, all have low numbers (50 or less). It should be noted that these evolutionary trends apply to the Malvaceae and do not necessarily reflect overall trends in the order. The mapping of these characters may change as more ingroup and outgroup taxa are added to the analyses.

Placement of certain taxa in the phylogenetic trees are of particular interest. Abelmoschus was formerly submerged in Hibiscus, but it is now generally treated as distinct (Kearney, 1951; Fryxell, 1997). In my cladistic analyses, Abelmoschus manihot is placed in a position closely related to the
two representatives of *Hibiscus*. *Pavonia strictiflora* was formerly *Goethea strictiflora* until it was returned to the genus *Pavonia* by Fryxell (1999). In my analyses, this species is the sister taxon to *Malvaviscus arboreus* and is more derived than the other closely related species of *Pavonia*. *Radyera farragei* was segregated out of *Hibiscus* by Fryxell and Hashmi (1971). My cladistic results may add some small amount of support to this separation in that *Radyera* does not form a clade with *Hibiscus*, but rather it appears to diverge earlier from the tree. In the molecular analyses by Seelanan, Schnabel, and Wendel (1997) the phylogenetic position of *Cienfuegosia* was ambiguous in the Gossypieae clade. My trees indicate that *Cienfuegosia ulmifolia* branches off prior to *Thespisia populnea* and *Gossypium hirsutum* in the clade.

**PLANS FOR FUTURE PROJECTS**

There are still many unresolved developmental issues in the Malvaceae that could not be addressed in the scope of the current research project. One of these is gynoecial development in *Palaua*, *Malope*, and *Kitaibelia*. These genera have gynoecia consisting of numerous carpels in complex arrangements. Because of this, these genera were once placed in a separate tribe called Maloeae (Kearney, 1951; Hutchinson, 1967). Currently, based on other morphological characters, these taxa are incorporated into the larger tribe Malvaeae (Bates, 1968; Bates and Blanchard, 1970). Much confusion has centered around the arrangement and ontogeny of carpels in these taxa. The numerous carpels have been described as arranged in two or more superposed or spirally arranged whorls (Kearney, 1951; Hutchinson, 1967) and as arranged in a pentagon (Payer, 1857; van Heel, 1995). In *Kitaibelia* and *Malope*, Payer (1857)
described the formation of five gynoecial humps (common meristematic mounds) on which carpel primordia initiate consecutively. Similarly, Endress (1981) stated that in *Kitaibelia* the gynoecium initiates as five primordia which each subdivide into a row of about 10 secondary primordia. Payer (1857) and Endress (1981) did not describe a carpel ring meristem. In contrast, van Heel (1995) asserted that in *Kitaibelia* and *Malope* the gynoecium first arises as a continuous girdling meristem. Subsequently the carpel primordia appear simultaneously. Further investigation is needed to determine the complete ontogeny and arrangement of carpels in these taxa.

My collection of *Abelmoschus manihot* is atypical in having ten carpels in the gynoecium, and these carpels are of two different sizes. More floral material needs to be examined to determine if the ten gynoecial primordia all initiate at the same time, or if they initiate as two sets similar to Malvavisceae. Flowers like this collection of aberrant *A. manihot* may help add insight about the transitions in the family from all fertile to some sterile carpels and in changes in carpel merosity, which can vary from three to numerous.

Position of the involucel in regard to the calyx is variable. In most taxa the bractlets are positioned in a whorl immediately adjacent to the calyx. There are, however, several exceptions to this. In the current research, *Anisodonta*ea *X hypomandarum*, *Thespesia populnea*, *Callirhoe involucrata* var. *involucrata*, and *Pachira aquatica* typically have one or more of the bractlets positioned slightly below the calyx on the receptacle. Similarly, four species of *Callirhoe* (Dorr, 1990), three species of *Anisodonta*ea (Bates, 1969), *Malvella leprosa* (Fryxell, 1988), *Thespesia beatensis*, *Lebronnecia kokioides*, and *Hampea rovirosae* (Fryxell, 1979) have one or more of the involucellar bractlets positioned below the calyx. *Anisodonta*ea *triloba* has
been described with five floral bract structures; the three structures that are closest to the calyx are involucellar bracts and the other two structures that appear further down on the pedicel are probably sterile bracts of the cyme according to Bates (1969). At the other extreme Callirhoe triangulata has bractlets that are sometimes adnate to the calyx (Dorr, 1990). Bates (1969) also reported that in Anisodonte anomala, the involucral bracts (involucellar bracts) are adnate to or joined with, or even form a single monophyllous whorl with the calyx. These species need to be examined to see if all the bractlet-like structures are actually bractlets, if they initiate on the floral apex, and how the structures become positioned at various levels.

Several other aspects of bractlet ontogeny deserve more attention. Bractlets are initiated, then suppressed in Thespesia populnea, Cienfuegosia ulmifolia, and in Pachira aquatica (Chs 3, 5). According to Fryxell (1979, 1988, 1997), most species of Cienfuegosia have an involucel; only four species (including C. ulmifolia) lack involucels. Fryxell reported the number of the bractlets (when present) in Cienfuegosia is typically nine to 12, rarely reduced to three due to coalescence or lateral connation. I found that C. ulmifolia only initiates three bractlet primordia and there is no evidence of more numerous primordia fusing to produce three. Fryxell's idea is one that needs to be further investigated for the other species of Cienfuegosia, and SEM would be a good tool to elucidate the bractlet ontogeny. It would be interesting to see if some species of Cienfuegosia have common bractlet primordia that trifurcate as is Radyera (Ch. 3). In addition, the other taxa that are described as lacking involucels should be examined to see if the bractlets are initiated and suppressed in some way as they are in C. ulmifolia.
and *T. populnea*. The suppressed bractlets in these taxa may be evidence of transitional stages in loss or gain of bractlets.

All of the taxa examined have helical initiation of bractlets on the floral apex, but it is more complex in *Radyera farragei*. In this species, rather than bractlet primordia initiating individually, common primordia initiate helically, then subsequently become lobed and divide. Payer (1857) suggested that the "calicule" (involucel) was formed by "bractées" and their accompanying "stipules"; thus they arise in groups of three (one large followed by two lateral smaller ones). The species in which Payer described this type of initiation should be reexamined with SEM to determine if the initiation pattern of the bractlets involves common primordia as in *Radyera* or helical initiation of individual primordia.

In the malvaceous taxa I examined, the androecium consists of one stamen whorl. There may, however, be exceptions to this in taxa that I have not examined. For example, *Sidalcea* is described with two series or phalanges of stamens (Fryxell, 1997). It should be noted that this report is not based on developmental data. An ontogenetic investigation of *Sidalcea* and perhaps some other taxa in Malvaceae is needed to discover if there are any true exceptions with more than one whorl of stamens in the androecium.

The foliar nectaries and stipular nectaries have received very little attention from morphologists. The foliar glands are usually localized on the base or near the base of the veins on the abaxial leaf surfaces and there are at least two morphological types (Fryxell, 1979, 1988). They are found in some species of *Urena, Decaschistia, and Hibiscus* and are characteristic of the Gossypieae (Fryxell, 1979). Stipular nectaries are unique in *Radyera*.
(Fryxell and Hashmi, 1971). SEM could be employed to discover how these nectaries develop and to detail their structure.

The nature of the gynoecium in Sterculia needs to be further investigated to determine the extent of development, timing of maturation, and the means of pollination in this species. My collection of Sterculia ceramica is unusual in the apparent lack of a fully mature gynoecium even at anthesis. Although the carpels develop locular cavities with ovules, the carpels remain relatively small, are included within the androecial tube, and lack any obvious stigmatic structure. I also did not see any evidence of temporary postgenital apical or subapical fusion of the carpels at anthesis that has been described for Sterculia by Cronquist (1981) and Endress, Jenny, and Fallen (1983). According to Bailey (1935), in this genus the early flowers are unisexual or polygamous (staminate, pistillate, and hermaphroditic flowers at the same time) and the late or terminal flowers are commonly pistillate. The collection of S. ceramica that I obtained is from a large tree that had numerous young inflorescences as well as some mature inflorescences and mature fruits. All of the flowers I examined had both male and female organs, but I did not see fully mature gynoecia (i.e. with significant enlargement and development of stigmatic surfaces). Other members of the Malvaceae (i.e. Napaea and some species of Hampea [Fryxell, 1997], and Callirhoe [Dorr, 1990]), have unisexual flowers which should be studied.

A feature that may be of taxonomic use is the presence of an endoglossum in some species (Kearney, 1951; Bates, 1969; Dorr, 1990). Two of the taxa I examined, Modiola caroliniana and Callirhoe involucrata var. involucrata, have an endoglossum. In the case of M. caroliniana it
divides each carpel into two chambers with an ovule in each. In C. *involucrata* it divides each carpel into a one-ovulate lower chamber and an upper sterile chamber. Bates (1969) presumed that some species of *Callirhoe*, *Urocarpidium*, and *Malvastrum*, which have uniovulate carpels and endoglossa, are the end product of a reduction sequence from pluriovulate carpels with endoglossa to uniovulate carpels with retained endoglossa. Fryxell (1988) cautions that the term has been applied to a variety of structures that may not be homologous. SEM and light microscopy could be used to investigate the homology and occurrence of these structures.

Clarification is needed concerning types of sterile structures in the androecia of Malvaceae, Bombacaceae, and Sterculiaceae. In Malvaceae and Bombacaceae the sterile structures (when present) are usually called sterile teeth, sterile appendages, sterile lobes, or less often staminodes or lobules; whereas in the Sterculiaceae the sterile structures (when present) are called staminodes (staminoids or sterile petaloid stamens). It is unclear what the distinction is between the terms sterile teeth and staminodes, and if these terms are applied correctly to the various members of these three families. The sterile parts terminating the androecial tube in some Malvaceae are described as mostly superseded in size by the fertile parts and insignificant as the flower reaches maturity (van Heel, 1966). Yet, some malvaceous taxa (*Malope trifida*, *Sphaeralcea umbellata*, *Lagunaria patersonii*, and *Thespesia populnea*) have well-developed sterile androecial parts that are relatively large at maturity (van Heel, 1966). The staminodes in sterculiaceous taxa are usually conspicuous; but there are exceptions with tiny staminodes, e.g. *Melochia umbellata* and *Hermannia candidans* (van Heel, 1966). Although not typical, some vascularization is found in the sterile...
teeth of malvaceous taxa, e.g. *Kokia rockii* and *L. patersonii* (van Heel, 1966) and in two varieties of *Hibiscus rosa-sinensis* (Saunders, 1936). The staminodes in most Sterculiaceae are described as vascularized, but there are a few exceptions (van Heel, 1966). So there does not appear to be a clear distinction between the sterile androecial structures in these families based on size or vasculature, but rather there appears to be gradation in size and amount of vasculature in the structures. Position of the sterile androecial structures is another issue. It was suggested that the sterile teeth in Malvaceae are the terminations of the antepetalous stamen whorl and that all traces of the antesepalous whorl are suppressed (Saunders, 1936). A contrary view would be that the sterile androecial parts are remnants of an inner stamen whorl in Malvaceae. Neither of these interpretations, however, can be used to generalize sterile androecial structures in all malvaceous taxa since the position of these structures varies among Malvaceae, being either antepetalous or alternipetalous (Ch. 2; van Heel, 1966) and sharing the same radii or not with the first-whorl stamen groups (Ch. 2). Also, *Bombax buonopozense*, *B. ceiba*, and *B. ellipticum* (Bombacaceae) have been described with sterile apical collars or sterile apical teeth in addition to two stamen whorls (van Heel, 1966). Obviously more research (position as well as vasculature and size) is needed to resolve homologies among these structures.

This research has established a basic framework of the floral ontogeny in Malvaceae. As the ontogeny of more taxa in the family and in the order are examined, characterization of the family and the tribes can be further refined. In addition, taxa that have been in questionable placement in a tribe or even in one of the core families can be examined. Some of the taxa which have
been in questionable placement include *Camptostemon, Quararibea, Fremontodendron, Cavanillesia, Hampea, Papuodendron, Durio, Bastardia, Bastardiopsis, Cephalohibiscus, Howittia,* and *Kydia* (Bates, 1968; Fryxell, 1968, 1969; Judd and Manchester, 1997). Comparison of their floral ontogeny and cladistic analysis will help to resolve the best placement for these genera and determine natural groupings for the taxa.

**CONCLUSIONS**

SEM has been a valuable tool to look at floral ontogeny and to show the ubiquity of certain floral developmental features among members of the Malvaceae. For example, all the representative taxa have a petal-stamen ring meristem resulting in the ontogenetic adnation of the petals to the androecium and the connation of the androecial members into a column. Petal elongation is delayed during stamen proliferation. The involucellar bractlets initiate on the floral apex whereas bracts or leaves initiate on the branch apical meristem. There appears to be a transition from helical initiation of organs in the outer organ whorl or whorls to simultaneous initiation in the inner organ whorls or organ sets. Ring meristems, when present in the bractlet, sepal, or carpel whorls, tend to be ambiguous. Also, common stamen primordia are prevalent in the young androecia.

This technique of examining ontogenetic series has also clarified development and homology of some of the unusual floral structures found in malvaceous flowers. For example, it has been illustrated that there are several ontogenetic pathways to the formation of the petal-stamen ring meristem, and that there is some variation in the partitioning and furcation events that occur in the androecium. The current work has refuted the idea that bifurcation and partitioning events are the likely causes of the
bisporangiate condition. It has been shown that there are several pathways to connation in the outer organ whorls and that presence of a ring meristem does not dictate organ connation at maturity. In some taxa, suppressed organs such as bractlets and sterile androecial teeth have been elucidated. Although a uniform ontogenetic pathway producing sterile teeth was not found, several factors were identified as sometimes contributing, and some were ruled out as causal. In the Malvavisceae, the initiation pattern, position, and subsequent fate of the sterile carpels was revealed. In addition, several unusual features have been shown such as the common bractlet primordia that occur in Radyera farragei and the displacement of bractlets in some taxa.

In addition to verifying diagnostic features of the tribes and characterizing the tribes, ontogenetic research has added insight into the systematics of the Malvaceae. Some ontogenetic characters are of value in distinguishing among the tribes and among certain genera. Cladistic analysis has shown that some but not all of the tribes are monophyletic and it has revealed several evolutionary trends in character traits. The use of ontogenetic characters can add to our understanding of natural groupings in Malvaceae and in the Malvales.

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DOCTORAL EXAMINATION AND DISSERTATION REPORT

Candidate: Teresa Shuff Crozier

Major Field: Botany

Title of Dissertation: Floral Ontogeny and Phylogeny in Malvaceae

Approved:

[Signatures of Major Professor and Chairman, Dean of the Graduate School, and EXAMINING COMMITTEE members]

Date of Examination: September 25, 2000

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