Comparative Inflorescence and Floral Development in the Asteraceae. (Volumes I and II).

Elizabeth M. Harris
Louisiana State University and Agricultural & Mechanical College

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Comparative inflorescence and floral development in the Asteraceae. (Volumes I and II)

Harris, Elizabeth M., Ph.D.
The Louisiana State University and Agricultural and Mechanical Col., 1991
Comparative Inflorescence and Floral Development
in the Asteraceae
Volume 1

A Dissertation

Submitted to the Graduate Faculty of the
Louisiana State University and
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Doctor of Philosophy
in
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by
Elizabeth M. Harris
B.A., University of Tennessee at Chattanooga, 1985
May 1991
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ABSTRACT

Floral and inflorescence development of 39 species of Asteraceae and four additional species representing possible outgroups were examined with the scanning electron microscope (SEM). Taxon choice was designed to include representatives of 12 of the 12 to 18 tribes recognized in the large, morphologically diverse family. Although floral ontogeny has provided phylogenetically useful characters in other plant groups, no similar studies have been applied to solve phylogenetic problems in the Asteraceae. The necessary live material was collected in several ways: from natural populations throughout North America, from the worldwide collections of several botanical gardens, grown from seed, or from cultivated specimens purchased from nurseries. For each species examined, several individual plants were sampled from each population, and in some cases, more than one population was sampled. Inflorescence and floral development was studied to document the range of variation possible among the developmental pathways of each species. Ontogenetic events were relatively stable within each species, when several individuals from either a single population or from different populations were sampled. Heterogamous heads consistently display suppression of peripheral (ray) flower initiation and development as compared to that of the disk flowers of the same head. Disk flowers and ray flowers of the same head are inherently dissimilar from initiation onwards, differing in size and shape of primordia, and in ensuing development. Several ontogenetic pathways were documented for the formation of ray flowers, receptacular bracts, and pappus; they appear to have phylogenetic significance. The corolla ring meristem was found throughout taxa of the subfamily Asteroideae but was absent from the Lactucoideae. Ligulate, bilabiate, and disk flowers throughout the Asteraceae display a high degree of similarity during early stages of development, but are dissimilar in late stages of corolla expansion. The pappus is initiated either during organogenesis with the other organ whorls, or substantially later during floral
expansion and differentiation as an achene outgrowth; the two modes of initiation are considered nonhomologous. If initiated during organogenesis, the pappus may form in one of three general patterns.
Review of Systematics Literature

Chapter 1
INTRODUCTION

The diverse family Asteraceae, with about 20,000 species in 1,100 genera, has cosmopolitan distribution (Cronquist, 1981). The family is characterized by the presence of capitulum-type inflorescences with subtending involucral bracts, anthers united in a tube, and often more than one type of flower on a single inflorescence, typically ray and disk forms. All flowers in the Asteraceae are epigynous, and are thus thought to be highly derived morphologically. An unusual structure, the pappus, has evolved to serve in seed dispersal (Cronquist, 1955; Jeffrey, 1985) and is putatively a calyx homolog. These characters (excluding epigyny) are autapomorphies (shared derived characters) for the family and provide strong evidence that the family is monophyletic (Cronquist, 1955; Bremer, 1987). Historically, systematics studies have been based on floral and vegetative morphology (Bentham, 1873; Cronquist, 1955; Sanders and Clark, 1987; Cox and Urbatsch, 1990), wood anatomy (Carlquist, 1966) and pollen ultrastructure (Bolick, 1978; Skvarla et al., 1977), as well as on cytological and chemical information (Vuilleumier, 1969).

Because of the large number of species in the family, the classification has long been the subject of considerable study and debate. Bentham's monumental work (1873), a definitive basis of knowledge for later workers, recognized the Asteraceae as having two sub-families and 13 tribes, on the basis of floral and vegetative characters. Most of Bentham's basic classification is still in use, with some modifications. Bentham's concept of two subfamilies was supported by Bremer's (1987) analysis, demonstrating the Cichorioideae as a grade (paraphyletic) and the Asteroideae as a clade.
(monophyletic). The sub-family Asteroideae was considered by Bremer (1987) as clearly monophyletic, although lacking resolution at several nodes in the consensus cladogram depicted (Bremer, 1987). However, the results he obtained were inconclusive on a global scale, due to the presence of many unnatural taxa (Bremer, 1987) in the classification system that he employed, the unavailability of character information, and the inclusion of numerous autapomorphic characters.

Since the 1950s, several workers have attempted to attain more natural groupings by critical analyses of the tribes and their phylogenetic interrelationships (Poljakov, 1967; Robinson and Brettell, 1973 a, b; Robinson and King, 1977; Turner and Powell, 1977; Jansen and Palmer, 1987, 1988). Bremer (1987) used data from the literature in a comprehensive cladistic study of tribal interrelationships.

In general, the phylogenetic relationships among the tribes are enigmatic, although some alliances among certain genera seem clear. Several tentative tribal alliances have been proposed by workers; there has also been speculation as to the ancestral or most primitive tribe. Cronquist (1955) concluded that Heliantheae, with a herbaceous habit, is the ancestral primitive tribe in the family and can be derived from the Campanulales.

Based on subsequent studies and conclusions by Carlquist (1976), Cronquist (1977) revised his idea, concluding that the ancestral habit was more likely to have been woody. Carlquist (1976) considered the Heliantheae, Vernonieae and Mutisieae to possess the greatest number of primitive features, but did not regard any extant group as ancestral within the family. By tabulating several morphological and anatomical characters, Wagenitz (1976) recognized two groups of tribes within the family, corresponding to the groupings in other studies (Robinson and Brettell, 1973a; Poljakov, 1967). Jeffrey (1977)
argued that the primitive corolla form was bilabiate, making the Mutisieae the primitive tribe within the family. Jeffrey's theory has been supported by the DNA studies of Jansen and Palmer (1987, 1988), which demonstrate the subtribe Barnadesiineae of the paraphyletic tribe Mutisieae (in the subfamily Cichorioideae) to be the basal or sister group to the remainder of the Asteraceae. The present work will use developmental data to test these hypotheses about relationships among tribes.

Recently, evidence from chloroplast DNA sequences and restriction site comparisons have placed the subtribe Barnadesiinae of the Mutisieae as outgroup to the rest of the family (Jansen and Palmer, 1987, 1988). While the family is monophyletic, some of the tribes and/or sub-tribal assemblages are paraphyletic groupings of convenience, awaiting further study (Bremer, 1987).

It has been hypothesized that the degree of ontogenetic divergence between two taxa is positively correlated with the degree of evolutionary divergence between the taxa (Stebbins, 1974; Gould, 1977; Tucker 1984). Comparison of an ontogenetic series among taxa (De Queiroz, 1985) in the inflorescence and floral ontogenies of the species examined, tests this hypothesis for the Asteraceae (Table 2.1). Selection of specific stages (the "semaraphonts" of Hennig, 1966) for comparison is also useful. Particularly useful are those stages that occur during earlier stages of ontogeny.
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Review of Developmental Literature

Chapter 2
INTRODUCTION

Research on the comparative development of inflorescence and floral morphology among tribes of the Asteraceae requires familiarity with both systematics and anatomical literature. In this review the floral anatomical literature is emphasized, although some systematics works are also discussed. The large number of studies have had many different aims—from horticultural flowering requirements to the classical anatomical studies describing histological phenomena. Developmental data for the inflorescence and/or flowers is thus often available from diverse sources and is collected here for comparative purposes.

Of the studies that approach the anatomy/development of the Asteraceae directly, the earlier works were generally of a comparative anatomical nature concerned with histological events and were based on study of serial sections with the light microscope. These studies were often broad in nature and several to many species were more or less perfunctorially examined. Sections were represented by camera lucida drawings (Haenlein, 1874; Warming, 1876) or freehand three-dimensional reconstructions (Payer, 1857; Koehne, 1869; Buchenau, 1872). Occasionally, observations were published without any pictorial representation of the material studied (Don, 1833; Trécul, 1890), leaving the reader to his own conclusions about the author's interpretations.

Later, life history studies involving intensive investigations of one or two genera became common (but see Lawalrée, 1948). Coulter (1883) examined the organogenesis and embryogenesis of the flowers of dandelion, Taraxacum officinale (Lactuceae). Martin (1892) examined development of the flower and
embryo-sac of Aster and Solidago (both Astereae). Five species of Silphium (Helianthae) were examined by Merrell (1900) and were shown to have similar floral initiation, organogenesis and embryogenesis. Farr (1913, 1915) investigated two species, Iva xanthifolia and Xanthium commune, of the Ambrosininae (a highly derived subtribe of the Helianthae). In an effort to understand flowering phenomenology of the important crop plant Lactuca sativa (Lactuceae), Jones (1927) investigated pollination and other details of the life history of lettuce. Morphological aspects of the life history were reported for weedy species such as Artemisia tridentata (Anthemideae) (Diettert, 1938), and Chrysothamnus nauseosus (Astereae) (Snow, 1945).

Floral vasculature has been compared in the Asteraceae for intrinsic information and for evidence of phylogeny. The initiation and development of floral vasculature of Tragopogon and Scorzonera (both Lactuceae) were studied by Trécul (1890), although without illustrations. Koch (1930, a, b) presented a definitive study of the vasculature of the corolla in the Asteraceae flower. In her initial study (1930a), she characterized four basic patterns of venation: the "Aster", "Helianthae", "Mutisieae", and the "discoid" types. After establishing these basic types, Koch (1930b) compared the vasculature of the Helianthae and the Mutisieae at some length, to test the theory (Haenlein, 1874; Small, 1917) that the ray flower developed from the bilabiate flower found in the Mutisieae. She found no support for this and concluded that the Helianthae were "anatomically primitive".

Philipson (1946, 1947a, b, 1948, 1953) investigated the developmental aspects of inflorescence morphology to ascertain possible relationships of the Asteraceae to other families (summarized in Philipson, 1953), presenting diagrams, camera lucida drawings, and micrographs. Philipson's investigations were twofold, involving the
comparative vasculature of the inflorescence and the histological events during the initiation of several structures. Concluding his studies of the nature of the Asteraceae inflorescence, Philipson (1953) grouped the Asteraceae inflorescence with those of the Campanulaceae, Calyceraceae, Goodeniaceae, and Stylidaceae which also show a racemose type of branching. He also established that, despite superficial similarities, the inflorescence of the Dipsacaceae is not homologous to the inflorescence of the Asteraceae.

The comparative study of the vascular supply of the corolla of both disk and ray flower was also applied taxonomically (Smith and Koch, 1935; Carlquist, 1957) by assessing the number and degree of branching in corolla veins. Rauh and Reznik (1953) documented the patterns of vasculature seen in developing inflorescences of the Asteraceae, Dipsacaceae and Campanulaceae in their histological study. While extremely useful, care must be taken when interpreting vasculature. Carlquist (1969) pointed out that erroneous conclusions may be drawn from vascular evidence. Manilal (1973, 1975), for example, erroneously asserted that capitula in the genus *Melampodium* (Heliantheae) were compound based on the vasculature of the bracts and was challenged by Burtt (1977). Other taxa, such as *Echinops*, clearly possess compound capitula (Petit, 1988).

Another group of investigations have been directed toward the physiological and photoperiodic requirements for flowering of Asteraceae (see the exhaustive reviews of the flowering requirements of horticulturally important Asteraceae in Halevy, 1985). The Asteraceae are historically important in these studies because *Xanthium* (Heliantheae) was one the first short day plants documented (Salisbury, 1985, and references therein). The literature is confusing because often contradictory reports of day-length requirements (Salisbury, 1985; Schuster, 1985) exist in the voluminous literature on
the subject, particularly among different cultivars of a species.

Two Asteraceae species predominate in studies of flowering: *Chrysanthemum morifolium* (Anthemideae) and *Helianthus annuus* (Heliantheae). Much information about the flowering requirements and genetics of *Chrysanthemum* is available--the plant has been in cultivation for more than 1400 years (Cockshull, 1985). The myriad mutations in color and form of both ray and disk flowers in *H. annuus*, as well as its simple cultural requirements, have made the plant popular as a subject for breeding experiments and inheritance studies (Fick, 1976; Schuster, 1985).

The first detailed ontogenetic study of an Asteraceae species was that of *C. morifolium* (Popham and Chan 1950, 1952) documenting the histological changes of an individual flower primordium and the vegetative apex during its transition to the inflorescence apex. They found (Popham and Chan, 1952; Popham, 1964) that the "crown bud," a large non-flowering bud found in *C. morifolium* under certain light regimens, was actually an inflorescence receptacle that did not initiate flower primordia. Popham (1964) extended the earlier work by sampling *C. morifolium* apices at regular intervals after exposing the plants to varying numbers of inductive photoperiods. In this way, he was able to show the stage of development in flower primordia of any age (in days). Cathey and Borthwick (1957) found that red light inhibited flower initiation and far-red light "repromoted" flower initiation in *Chrysanthemum*. Disturbing (by defoliation, bisection, or puncturing) the transition apex of *Petasites hybridus* (Senecioneae), Wardlaw (1963) caused the apex to revert to the vegetative condition. Formation of the first involucral bract heralds the irreversible reversion of the *Chrysanthemum* inflorescence meristem back to a vegetative state (Horridge and Cockshull, 1979). Synthesizing earlier works, Charles-
Edwards et al. (1979) developed a mathematical model of flowering for *C. morifolium*.

Among many studies of the genetics and flowering of *Helianthus annuus* (Heliantheae) (Schuster, 1985 and references therein), of particular interest is the work of Marc and Palmer (1976, 1978a, 1978b, 1981) who have used an experimental approach to the mechanisms of flowering in certain cultivars of sunflowers. They established that inflorescence development was sensitive to water stress (Marc and Palmer, 1976) as shown by the decreased number of flowers initiated on the head, but that the timing of the onset of the flowering response was not affected. Marc and Palmer (1978a) were able to use chilling pulses to determine the duration of events leading to flowering by standardizing the timing of flowering. They (1978b) found that six or seven flower primordia per day were initiated on the meristematic surface of the inflorescence in the *Helianthus* cultivars they studied. A boron deficiency produced an unusual effect (simulated by wounding of the inflorescence meristem, Palmer and Marc, 1982): cracks in the meristematic surface along which new involucral bracts, ray flower primordia, then disk flower primordia were produced, in that order.

Genetic studies of several aspects of flowering in certain Asteraceae species are a relatively recent area of research. Most notably, Bachmann and Chambers (1990, and references therein) and their coworkers have described genetic variation in *Microseris* (Lactuceae) through hybridization studies. By investigating the phenotypic expression of meristic characters (such as pappus part number, or the ratio of dimorphic achenes on a head) Bachmann and Chambers (1990, and references therein) were able to determine evolutionary factors that change or stabilize (canalize) (Stebbins, 1974) these morphological structures in *Microseris* (Lactuceae) hybrids. Gottlieb and Ford (1989, and references therein) investigated
the presence of ray flowers in two sister species of *Layia* (Heliantheae). Through hybridization studies, it was found that only two genes were involved in coding for the presence of ray flowers in *L. glandulosa*, and that *L. discoidea*, while lacking rays, retained genes that modify ray number and color.

New technology augmented the capabilities of light microscopy and heralded a renaissance in the study of floral development, and the Asteraceae were not ignored. Sattler (1973) extended the limits of the dissection microscope with his system of epi-illumination and dipping cones. In the photographic text-atlas *Organogenesis of Flowers*, Sattler (1973) examined floral development in 50 species in 44 families, including *Tragopogon pratensis* (Lactuceae) and *Tagetes patula* (Heliantheae) from the two subfamilies in the Asteraceae.

The scanning electron microscope (SEM) has become the instrument of choice for many developmental morphologists because of increased resolution and depth of field. Marc and Palmer (1978b, 1981) used the SEM extensively to document stages in the flowering of *H. annuus*. The floral initiation and development of two horticulturally important Inuleae species, *Helipterum roseum* and *Helichrysum bracteatum*, were also studied (Sharman and Sedgley, 1988). Harris et al. (1991) described bidirectional flower initiation and development for *Erigeron philadelphicus* (Astereae), contrary to the generally reported acropetal (or centripetal) pattern for the Asteraceae.

The reduction of heads to second order capitula, "synflorescences", "syncephalia", or "incapitulescences" in some species of the Asteraceae is generally accepted (Kunze, 1969; Burtt, 1977; Froebe and Classen 1987; Petit, 1988). By documenting initiation of individual flowers and flower groups with the SEM, Classen-Bockhoff et al. (1989) suggested that the inflorescence of *Gundelia tournefortii* (Arctoteae) is derived from a tertiary reduction of heads. In other words, one
or few flowered heads are condensed into second-order heads, which are then condensed again into third-order heads, a state also recorded for the aptly named *Triplocephalum* (Inuleae) (Burtt, 1977).

The ongoing SEM investigations by Leins and his coworkers are impressive for their scope both in the Asteraceae (see below) and in other families (Erbar and Leins, 1988, 1989; Leins and Erbar, 1989). Leins and Gemmeke (1979) showed compelling evidence for the secondary inflorescence condensation in *Echinops exaltatus* (Cynareae), although they were reluctant to make that assertion unequivocally.

Expanding their studies in the Asteraceae, Leins and Erbar (1987) presented a large study of 17 Asteraceae species (although SEM and light microscope micrographs from only five of the species were published). The primary aim of the paper was comparison of flower development, particularly the formation and growth of the corolla tube *sensu lato*. Based on their SEM studies of floral development of the Asteraceae and five related families, Leins and Erbar (1990) postulated a putative phylogenetic [sic] arrangement of the secondary pollen presentation mechanisms of the six families under consideration. The Asteraceae "brush" and "pump" mechanisms were hypothesized to be derived from hypothetical ancestral state that combined the pollen deposition and brushing techniques.

Moncur (1981), using the SEM, investigated floral initiation of temperate field crops. Five Asteraceae species were included in the his study: *Helianthus annuus* (Heliantheae), *Carthamus tinctorius* (Cynareae), *Guizotia abyssinica* (Heliantheae), *Parthenium argentatum* (Heliantheae), and *Lactuca sativa* (Lactuceae). Common primordia were shown in *Helianthus annuus* that bifurcated after initiation to flower primordia adaxially, and receptacular bract primordia abaxially. In those species possessing ray flowers, the
developmental lag was also evident between the ray flowers and disk flowers. *Chrysanthemum morifolium* was also a subject for SEM studies, expanding knowledge about flowering of this horticulturally important Asteraceae species (Horridge et al., 1985).

**EVENTS IN INFLORESCENCE DEVELOPMENT**

The direction of flower initiation and development on the capitulum is a useful character for interpreting homologies and relationships with other families. An Asteraceae head is a condensed determinate inflorescence (Cronquist, 1955), believed to be derived from either a contracted raceme directly (Cronquist, 1977; Jeffrey, 1977; Weberling, 1989), or from a racemose umbel (Small, 1918; Stebbins, 1974). Part of the evidence for these essentially similar interpretations is the order of flowering (anthesis) on the head, usually described as uniformly centripetal (Payer, 1857; Cronquist, 1977; Burtt, 1977). The determinate nature of the Asteraceae inflorescence is supported by the general lack of an identifiably terminal flower or other structure on the capitulum (Lawalrée, 1948). Only rarely are terminal flowers found, and they are interpreted as the consequence of a secondary condensation of heads (Leins and Gemmeke, 1979; Classen-Bockhoff et al. 1989).

**Sequence of floral initiation**—Many authors have provided solid evidence for the strictly acropetal, or centripetal, direction of flower initiation on the surface of the inflorescence meristem. Explicitly stated or portrayed acropetal floral initiation in micrographs or camera lucida drawings have been shown for: *Taraxacum officinale* (Coulter, 1883); *Solidago* (Martin, 1892); *Xanthium* (Farr, 1915;
Salisbury, 1985); **Lactuca sativa** (illustrated as acropetal in Jones, 1927, although called simultaneous in text; Moncur, 1981); **Bellis perennis** (Philipson, 1946); **Galinsoga parviflora** (Lawallée, 1948); **Zinnia hageana**, **Crepis rubra**, and **Centaurea cyanus** (Rauh and Reznik, 1953); **Helianthus annuus** (Marc and Palmer, 1978b, 1981); **Echinops exaltatus** (Leins and Gemmeke, 1979); **Tussilago farfara** (Wardlaw, 1961); **Carthamus tinctorius** (Moncur, 1981); **Calendula arvensis** (Hilger and Reese, 1983); **Chrysanthemum morifolium** (Popham and Chan, 1952; Horridge et al. 1985); **Dimorphotheca pluvialis**, and **Osteospermum vaillantii** (Reese and Hilger, 1984), and **Helipterum roseum** and **Helichrysum bracteatum** (Sharman and Sedgley, 1988).

The phenomenon of delayed ray flower initiation until after the disk flowers have already begun to develop (i.e., not strictly acropetal/centripetal) has been recorded only rarely: **Cosmos bipinnatus** (Molder and Owens, 1973, 1985) and **Erigeron philadelphicus** (Harris et al., 1991) or merely depicted, but not commented upon, for **Silphium** (Merrell, 1900).

**Sequence of floral development**—Following initiation, the sequence of subsequent development among the flowers on a head has often been shown to follow an acropetal pattern. **Solidago** (Martin, 1892), **Iva xanthifolia** (Farr, 1913), **Crepis rubra**, and **Centaurea cyanus** (Rauh and Reznik, 1953), **Lactuca sativa** (Jones, 1927; Moncur, 1981), **Carthamus tinctoria** (Moncur, 1981), and **Helipterum roseum** and **Helichrysum bracteatum** (Sharman and Sedgley, 1988) all possess homogamous heads that show uniformly acropetal (centripetal) development on the head.

There are numerous examples of variations on the strictly acropetal course of development on the head; e.g. where there is a lag of the ray flowers or other peripheral flower primordia, compared to the remaining, central disk flower
primordia in the sequence of development on the head. In this pattern, the ray flower primordia are initiated but then are suppressed (or become dormant) so that subsequently initiated disk flower primordia outstrip the rays in both size and stage of development. This may be seen in: Calendula officinalis (Payer, 1857); Calendula arvensis, Dimorphotheca pluvialis, and Osteospermum vaillantii (Reese and Hilger, 1984); Silphium (Merrell, 1900); Chrysanthemum morifolium (Horridge et al., 1985); Chrysanthemum leucanthemum, Galinsoga parviflora (Lawalrée, 1948), Bellis perennis (Philipson, 1946; Lawalrée, 1948); Tussilago farfara (Wardlaw, 1961); and Erigeron philadelphicus (Harris et al., 1991).

Other sequences of overall floral development (and anthesis) though rare, usually indicate a condensation of heads: Echinops exaltatus (Leins and Gemmeke, 1979); E. sphaerocephalus (Kruse and Meusel, 1969; Kunze, 1969); Syncephalantha decipiens, and Myriocephalus gracilis (Kunze, 1969). The "flower groups" of Gundelia tournefortii (Classen-Bockhoff et al., 1989) develop basipetally in each group, but the groups on the head develop in an overall acropetal sequence.

EVENTS IN FLORAL DEVELOPMENT

The order of organogenesis in the Composiatae is generally corolla first, then stamens, and finally gynoecium (Table 2.1). The pappus, if also present, may appear at any stage during organogenesis, but is rarely initiated as the first organ set.

The appearance of individual organs within each whorl or set is generally simultaneous (Leins and Erbar, 1987; Harris, pers. obs.). Non-simultaneous initiation of members of an organ whorl is occasionally mentioned for carpels (Haenlein, 1874; Lawalrée, 1948), and for stamens and pappus members
(Sattler, 1973). If a ring meristem precedes the appearance of subsequent members of an organ whorl such as corolla lobes or pappus members, initiation is regarded as simultaneous. An example is seen in the corolla lobes of *Erigeron philadelphicus* (Harris et al., 1991), which are differentiated from the corolla ring meristem in a unidirectional sequence.

**SUMMARY**

The large natural family Asteraceae has interesting problems for systematists, anatomists and morphologists, particularly in the study of inflorescence and floral development. Developmental information is often produced by studies that have other goals. Initially, anatomists studying development used the light microscope and concentrated on vasculature and histological events. More recently, developmental biologists have employed the SEM, often in conjunction with the light microscope.

The historical characterization of floral initiation and development on the Asteraceae head as uniformly acropetal/centripetal is not entirely accurate. Non-acropetal events have been recorded in some taxa, although they have not always been recognized as such. Often, but not always, non-acropetal events indicate the presence of a secondarily reduced inflorescence.

A particular order of initiation; i.e., corolla, stamens, and gynoecium, is canalized throughout the family. The pappus, however, has a variable onset of initiation across the family (but is consistent in timing within any particular species). Organs in a whorl are generally initiated simultaneously, with few exceptions.
Table 2.1. Organogenetic sequences for Asteraceae.

<table>
<thead>
<tr>
<th>Species</th>
<th>Tribe</th>
<th>Disk fl.</th>
<th>Ray fl.</th>
<th>Reference</th>
</tr>
</thead>
<tbody>
<tr>
<td><strong>Subfamily: Asteroideae</strong></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td><em>Achillea millefolium</em></td>
<td>Ant</td>
<td>ng</td>
<td>Co,G</td>
<td>Leins &amp; Erbar, 1987</td>
</tr>
<tr>
<td><em>Artemisia tridentata</em></td>
<td>Ant</td>
<td>Co,S,G</td>
<td></td>
<td>Diettert, 1938</td>
</tr>
<tr>
<td><em>Aster sp.</em></td>
<td>Ast</td>
<td>Co,S/P,G</td>
<td>ng</td>
<td>Martin, 1892</td>
</tr>
<tr>
<td><em>Chrysothamnus nauseosus</em></td>
<td>Ast</td>
<td>Co,S,P,G</td>
<td>(discoid)</td>
<td>Snow, 1945</td>
</tr>
<tr>
<td><em>Erigeron philadelphicus</em></td>
<td>Ast</td>
<td>Co,P,S,G</td>
<td>Co,P,G</td>
<td>Harris et al., 1991</td>
</tr>
<tr>
<td><em>Solidago sp.</em></td>
<td>Ast</td>
<td>Co,S/P,G</td>
<td>(discoid)</td>
<td>Martin, 1892</td>
</tr>
<tr>
<td><em>Calendula arvensis</em></td>
<td>Cal</td>
<td>ng</td>
<td>Co,G</td>
<td>Hilger &amp; Reese, 1983</td>
</tr>
<tr>
<td><em>Calendula arvensis</em></td>
<td>Cal</td>
<td>Co,S,G</td>
<td>Co,G</td>
<td>Reese &amp; Hilger, 1984</td>
</tr>
<tr>
<td>Species</td>
<td>Tribe</td>
<td>Disk fl.</td>
<td>Ray fl.</td>
<td>Reference</td>
</tr>
<tr>
<td>------------------------------</td>
<td>-------</td>
<td>----------</td>
<td>---------</td>
<td>--------------------</td>
</tr>
<tr>
<td>Calendula officinalis</td>
<td>Cal</td>
<td>ng</td>
<td>Co,S,G,P</td>
<td>Leins &amp; Erbar, 1987</td>
</tr>
<tr>
<td>Ambrosia maritima</td>
<td>Hel</td>
<td>Co/G</td>
<td>ng</td>
<td>Payer, 1857</td>
</tr>
<tr>
<td>Bidens frondosa</td>
<td>Hel</td>
<td>Co,S,P,G</td>
<td>ng</td>
<td>Leins &amp; Erbar, 1987</td>
</tr>
<tr>
<td>Coreopsis sp.</td>
<td>Hel</td>
<td>Co,P,S,G</td>
<td>Co,P,S,G</td>
<td>Scheefer-Pomplitz, 1956</td>
</tr>
<tr>
<td>Gaillardia sp.</td>
<td>Hel</td>
<td>Co/P,S,G</td>
<td>Co,P,S,G</td>
<td>Scheefer-Pomplitz, 1956</td>
</tr>
<tr>
<td>Helianthus sp.</td>
<td>Hel</td>
<td>Co,P,S,G</td>
<td>Co,P,S,G</td>
<td>Scheefer-Pomplitz, 1956</td>
</tr>
<tr>
<td>Heliopsis scabra</td>
<td>Hel</td>
<td>Co,P,S,G</td>
<td>Co,P,S,G</td>
<td>Payer, 1857</td>
</tr>
<tr>
<td>Silphium spp.(5)</td>
<td>Hel</td>
<td>Co,S,G,P</td>
<td>Co,S,G,P</td>
<td>Merrell, 1900</td>
</tr>
<tr>
<td>Tagetes patula</td>
<td>Hel</td>
<td>Co,P,S,G</td>
<td>Co,P,S,G</td>
<td>Sattler, 1973</td>
</tr>
<tr>
<td>Xanthium commune</td>
<td>Hel</td>
<td>female: Co,G</td>
<td></td>
<td>Farr, 1915</td>
</tr>
<tr>
<td></td>
<td></td>
<td>male: Co,S,G</td>
<td></td>
<td></td>
</tr>
</tbody>
</table>
Table 2.1. continued

<table>
<thead>
<tr>
<th>Species</th>
<th>Tribe</th>
<th>Disk fl</th>
<th>Ray fl</th>
<th>Reference</th>
</tr>
</thead>
<tbody>
<tr>
<td><strong>Cichorium intybus</strong></td>
<td>Lac</td>
<td>Co,S,P,G (ligulate)</td>
<td>Moncur, 1857</td>
<td></td>
</tr>
<tr>
<td><strong>Cichorium intybus</strong></td>
<td>Lac</td>
<td>Co,S/P,G (ligulate)</td>
<td>Payer, 1857</td>
<td></td>
</tr>
<tr>
<td><strong>Microseris douglasii</strong></td>
<td>Lac</td>
<td>Co,S/P,G (ligulate)</td>
<td>Leins &amp; Erbar, 1987</td>
<td></td>
</tr>
<tr>
<td><strong>Lactuca sativa</strong></td>
<td>Lac</td>
<td>Co,S/P,G (ligulate)</td>
<td>Jones, 1927</td>
<td></td>
</tr>
<tr>
<td><strong>Lactuca sativa</strong></td>
<td>Lac</td>
<td>Co,S/P,G (ligulate)</td>
<td>Moncur, 1981</td>
<td></td>
</tr>
<tr>
<td><strong>Taraxacum officinalis</strong></td>
<td>Lac</td>
<td>Co,S,G,P (ligulate)</td>
<td>Coulter, 1883</td>
<td></td>
</tr>
<tr>
<td><strong>Tragopogon pratensis</strong></td>
<td>Lac</td>
<td>Co,S,G/P (ligulate)</td>
<td>Sattler, 1973</td>
<td></td>
</tr>
</tbody>
</table>

Subfamily: Cichorioideae
Table 2.1. continued

Co = Corolla
S = Stamens
P = Pappus
G = Gynoecium
/
= indicates simultaneous initiation
*  = occasionally noticed
ng = not given in the study
(ligulate) = spp. with ligulate flowers only
(discoid) = spp. with disk flowers only

Organogenetic sequences to be read from left to right; i.e. Co, S, P, G indicates that the corolla initiates first, stamens next, then the pappus and finally the carpels.


Don, D. 1833 (read 1828). On the origin and nature of the ligulate rays in Zinnia; and on a remarkable multiplication observed in the parts of fructification of that genus. The Transactions of the Linnean Society of London. Botany. 16: 155-158.


Floral Initiation and Early Development in *Erigeron philadelphicus* (Asteraceae)

Chapter 3

By Elizabeth M. Harris, Shirley C. Tucker, and Lowell E. Urbatsch

Feb 1, 1991

Dear Dr. Harris,

You have permission to have 25% re-microfilm your dissertation, including the Euphues ms.

Sorry for the delay in responding.

Anne Richarte
Assistant to the Editor,
American Journal of Botany

Re "Floral initiation and early development in Euphues philadelphica (Asteraceae)"
ABSTRACT

The order of floral initiation and subsequent organogeny of *Erigeron philadelphicus* L. (Asteraceae: Astereae) was found to deviate from the acropetal pattern generally reported for the Asteraceae. Light micrographs show periclinal divisions in the first, second, and deeper subsurface layers of cells on the flanks of the inflorescence apex as the earliest evidence of floral initiation. Scanning electron microscope micrographs indicate that the disk flowers appear first and arise as small protuberances approximately one-third of the way up the previously undifferentiated highly convex inflorescence apex. A succession of disk flowers arises acropetally in a complex anthotaxy characterized by about 21 dextrorse and 12-15 sinistrorse parastichies (although this pattern is obscured at the apex). After one to three disk flowers have been initiated in each parastichy, the first ray flower initials can be seen to initiate in sites proximal to the oldest and largest disk flowers. Additional ray flowers then initiate basipetally following the dextrorse parastichies established by the disk flowers. Overall floral initiation on the inflorescence apex proceeds acropetally for the disk flowers and basipetally for the ray flowers until the available space is filled. Floral development adheres to the same plan—proceeding bidirectionally on the inflorescence meristem with the oldest and most complete flowers of both types located on the equator established at initiation.
INTRODUCTION

Floral initiation, development, and anthesis of Asteraceae are generally described as occurring in an acropetal or centripetal direction on the capitulum (Payer, 1857; Buchenau, 1872; Haenlein, 1874; Philipson, 1946; Lawalrée, 1948; Cronquist, 1955, 1977; Sattler, 1973; Reese and Hilger, 1984). The inflorescence is generally viewed as being reductively derived from a contracted raceme (Burtt, 1977; Jeffrey, 1977; Stebbins, 1977). Floral initiation begins with primordia arising immediately distal to the uppermost (most recently formed) involucral bracts and then continues acropetally. In radiate species (possessing both ray and disk flowers) that have been described (Popham and Chan, 1952; Moncur, 1981; Hilger and Reese, 1983; Leins and Erbar, 1987), the prescribed number of rays is produced first (inflorescence A in Fig. 1), and then with little or no transitional floral forms, the outermost disk flowers are initiated in continuous acropetal initiation until the inflorescence apex is filled. Generally, subsequent development and anthesis on the capitulum follow the order established at floral initiation (Philipson, 1946; Marc and Palmer, 1978).

A comparative study of inflorescence and floral ontogeny of members of the Asteraceae is under way [employing the scanning electron microscope (SEM) and sectioned buds for the light microscope] of which this work is a part (Harris, unpublished data). The objective of this overall project is to explore inflorescence development, floral initiation, and early development in representative species of each tribe of the Asteraceae. Results from Erigeron philadelphicus are presented here separately to document previously unrecorded
patterns of floral initiation and development found in this species. The larger overall study is designed to test and to have applications on several levels: 1) Record patterns of floral ontogeny that test tribal, or other, delimitations; 2) Test classical hypotheses of Asteraceae floral ontogeny, such as the uniform distribution of acropetal floral initiation and development in the family (Payer, 1857; Buchenau, 1872; Haenlein, 1874); 3) Investigate the morphological causes and effects of instances of heterochrony, suppression, and other developmental phenomena in the Asteraceae. As inflorescence and floral development are recorded for individual species representing different tribes, developmental pathways characteristic of higher orders in the Asteraceae should become evident.

MATERIALS AND METHODS

Material of *E. philadelphicus*, a biennial or short-lived perennial species widespread throughout North America (Cronquist, 1980), was collected in February 1986 from the campus of Louisiana State University, Baton Rouge, Louisiana. Inflorescences of all ages were fixed in formalin-acetic acid-alcohol (FAA: 90 cc 50% ethanol: 5 formalin: 5 acetic acid). Voucher specimens (Elizabeth Harris #117) were deposited in the Louisiana State University Herbarium (LSU). The preserved material was dissected and examined in 95% ethanol, dehydrated in an alcohol/acetone series, and critical-point dried in a Denton DCP-1. Specimens were then mounted on SEM stubs and coated with gold-palladium in a Hummer II sputter-coater. The prepared floral material was studied with a Hitachi S-500 SEM at 25 kV and representative micrographs were made.
For sectioning, preserved material was dehydrated in tertiary-butyl alcohol and embedded in "Paraplast." Sections were cut 7 μm thick with a rotary microtome, mounted on slides, and then stained sequentially with safranin and alcian green, modified from Joel (1983), for study with the light microscope.

The use of SEM in addition to light microscope findings has proven to be valuable, and occasionally indispensable, for developmental studies. One of the main difficulties encountered in the present study relates to the limits of tissue sectioning. While obtaining a median section of an inflorescence is possible, individual flowers may or may not be median. In addition, even if the entire section is median, it is impossible for all the flowers of any particular parastichy to appear in one section due to the angle of the parastichies' ascendance on the inflorescence (Fig. 1), unless, of course, one managed to section at precisely that angle rather than parallel to the axis. Thus, one may obtain sections with a few median flowers, surrounded by flowers that are just nonmedian to barely glancing. Depending on the section chosen, almost any sequence of initiation could be demonstrated. Clearly, for comparative inflorescence-wide events, light microscope sections are not enough. With the three-dimensional image attainable with the SEM, however, inflorescence events are easily noted and recorded. The two techniques complement each other for a more complete elucidation of inflorescence and floral ontogeny.

Terms--As unique developmental events occur in *E. philadelphicus*, new terminology is necessary to facilitate description and discussion. The "equator of origin" or simply "equator" is defined as the encircling zone on the inflorescence which gives rise to disk flowers distally and ray flowers proximally (dotted line on inflorescence B in Fig. 1). The term "bidirectional" as used here applies to initiatory and
developmental events of all flowers on an inflorescence and not to organogenesis of an individual flower. Thus, the pattern of simultaneous acropetal and basipetal floral initiation and development originating from the equator is called bidirectional (inflorescence B in Fig. 1), in contrast to the strictly acropetal or centripetal pattern (inflorescence A in Fig. 1) found in most Asteraceae reported.

RESULTS

**General habit**—*E. philadelphicus* emerges in the early spring as a basal rosette. Eventually the shoot bolts, producing the elongate main axis which attains an average height of 50 cm in the population studied. The usually solitary axis bears a terminal inflorescence and several secondary inflorescences (Figs. 2, 3, 4). At anthesis, the inflorescences are 15-20 mm broad, with no distinction in size between the terminal and secondary inflorescences. Each secondary inflorescence is initially borne in an inflorescence bract axil (Figs. 3, 4), but as the inflorescence approaches anthesis the peduncle elongates leaving the bract below. Development of the inflorescences on the plant axis begins with the terminal inflorescence and proceeds basipetally (Fig. 4). This sequence corresponds to the simplest synflorescence groundplan of the Asteraceae, a paniculodium (Kunze, 1969), in which each inflorescence is borne independently and the terminal inflorescence is the first to undergo anthesis which then proceeds basipetally down the axis. Approximately 270 disk flowers and 310 ray flowers were produced on a single capitulum in the study population.

The pentamerous disk flowers are perfect and fertile, with uniformly yellow corollas, exhibiting radial symmetry. Disk corollas (including the tube and individual lobes) are 2.5-3 mm
long and 0.3-0.5 mm wide at anthesis. The ray flowers are pistillate, fertile, and white to pink/lavender. Ray flower corollas are bilaterally symmetrical with a strap-like ligule at anthesis resulting from the differential enlargement of the abaxial portion of the corolla. Ray corolla limbs are 5.5 to 6 mm long, tube length is 2-2.5 mm for a total of 7.5-8 mm for the entire ray corolla. Lacking in the ray flowers are stamens and any indication of corolla lobes or teeth. Both floral types produce fertile achenes which measure 0.5-0.75 mm long and 0.1 mm wide, and each achene bears a pappus of numerous simple bristles.

Inflorescence development--The first floral primordia are initiated when the inflorescence apex is in the range of 325-450 μm in diameter and 190-255 μm in height (Figs. 5, 6); location of the primordia indicates that they are the outermost disk flowers. The darkly staining (Figs. 4, 6) surface meristematic layers that overlay a highly vacuolate core correspond to Gregoire's (1938) inflorescence mantle layers. Primordia arise on the flank of the hemispheric inflorescence apex at the equator, about one-third to one-half of the distance from the base of the inflorescence at the level of involucral bracts to the tip of the hemispheric inflorescence apex. In Figs. 5 and 6, the first disk flowers are initiating; in Fig. 7, several are present over the surface. Subsequent disk flowers are then initiated acropetally along low-angle parastichies. Numerous disk flower primordia are formed over the surface in quick succession, before earlier ones enlarge. After the initiation of one to three disk flowers, the first ray primordia are initiated proximally or basipetally to the lowermost and oldest disk flowers (Fig. 7) in the meristematic band which encircles the inflorescence below the equator. Further initiation of ray flower primordia proceeds basipetally to fill the remaining meristematic space (Figs. 1b, 9, 11) between the equator and the region of involucral bract primordia. An individual parastichy ultimately includes from
five to eight ray flowers (Figs. 9, 12, 38) which continue the same 21 dextrorse parastichies established by the disks (Fig. 12). While 12-15 sinistrorse parastichies may be delimited for the disk flowers (Fig. 13); ray flowers do not consistently adhere to the parastichies in this direction. While the ray flowers are initiating basipetally, disk flowers continue to be initiated in an acropetal order and eventually "use up" the inflorescence apex. As the parastichies converge on the apex of the inflorescence, individual parastichies merge, obscuring their pattern. No one flower can be said to be in a strictly terminal position (Fig. 13), rather, the terminal flowers of each parastichy compete for the limited space available. Enlargement of the surrounding primordia soon obscures (Fig. 14) the remaining uncommitted inflorescence meristem (Fig. 13, arrow) which is presumably too small to produce another floral primordium.

Floral development on the inflorescence follows the bidirectional pattern established during initiation--the first flower primordia to initiate organogenesis are those located closest to the equator with organogenesis radiating outward from this line in a bidirectional fashion (Fig. 12). The oldest, most basal disk flowers located on the equator begin organogenesis. The organogenesis of disk flowers then proceeds acropetally on the capitulum (Figs. 12, 13). Successively younger and more central disk flowers are always at correspondingly earlier stages of development than the basal ones (Figs. 12, 13). In both floral types, the oldest and largest primordia, located on the equator, are the first to initiate organogenesis.

The onset of organogenesis for the ray flower primordia is delayed in E. philadelphicus, producing a definite lag in development of ray flowers (Figs. 12, 28, 30) behind that of disk flowers of the same age. Organogenesis in the ray flowers does not begin until the adjacent disk flowers at the
equator have already enlarged and produced corolla lobes, pappus, and stamen primordia (Figs. 28, 42).

**Disk flower development**—Floral primordia are initiated by periclinal divisions in the first and second subsurface layers of the inflorescence (Figs. 6, 8, arrow) and will become the outermost disk flowers. Relative sizes of both disks and rays at comparable stages in development are given in Table 3.1. After initiation, the floral primordia expand into rounded protuberances by more randomly oriented cell divisions in the first, second, and third subsurface layers (Figs. 10, 11). The primordia then become flat apically (Figs. 15, 16, left flower)—the "plug" stage (Erbar, 1988). A ring meristem forms (Figs. 15, 16, right flower), resulting in the formation of an apical indentation (Figs. 15, 16). Five distinct swellings on the corolla ring meristem appear in rapid succession, but not synchronously, to become the corolla lobe primordia (Fig. 17, flower in right foreground) by means of subapical initials (Figs. 16, 18, arrows). First to appear is the abaxial corolla lobe primordium (Fig. 12, arrow labelled "A") located on the flower's median longitudinal plane. Next to appear are the two lateral corolla lobe primordia (Fig. 12, arrow labelled "L"). Last to appear are the two adaxial primordia (Fig. 12, arrow labelled "X"). Action of the subapical initial (Fig. 16, arrows) produces short files of cells (Fig. 18) which causes the corolla lobes to expand into erect bulges which then arch inwards covering the interior of the flower (Figs. 21-24).

After the corolla ring meristem is present, the pappus ring meristem appears. Periclinal divisions in the first subsurface layer encircling the flower midway between the base and apex of the floral primordium preceded by cell enlargement (arrow in Fig. 20; Fig. 18 shows an earlier stage with some cell enlargement) are the first evidence of the pappus ring meristem. The pappus briefly remains as an undifferentiated ring meristem, seen externally (arrow, Figs. 17, 19) as a slight
bulge girdling the flower midway. The primordial pappus ring meristem quickly differentiates to produce numerous individual primordia synchronously (Figs. 21, 23), which become the individual pappus bristles (Figs. 26, 27).

The five stamen primordia arise synchronously very soon after the pappus, or in some cases overlapping with the inception of the pappus ring primordium. Stamen initiation results from periclinal divisions in the subsurface layer (Fig. 20). The stamen primordia alternate with the corolla lobe primordia and are located on the sides of the concave floral apex (Fig. 19) which remains meristematic (Fig. 20).

The last organs to form are the two carpels. The carpels are initiated (Fig. 22, arrow) on the sides of the concave floral apex below the stamens, and lie on the median plane of the flower. Initially free (Fig. 22), the carpels enlarge and become appressed (Fig. 24) at about the time that the individual pappus primordia begin to enlarge (Figs. 23, 24). The apices of the two carpels elongate by general cell division (Figs. 25, 26), remaining appressed but not fusing at this time. One ovule per flower is initiated basally (Fig. 25) in the single joint locule of the carpels. The ovule is anatropous (Fig. 27) and has one integument. Further development of the ovule was not followed.

Ray flower development--The first recognizable ray primordia on the inflorescence surface are noticeably smaller than the disks at the equator (Table 3.1; Figs. 9-11). This disparity in size between disk and ray flowers is maintained during early developmental stages (Figs. 10, 11). Only shortly before anthesis does the ray corolla expand and overtake the disks in length (Fig. 14). Initiation of ray flower primordia begins with periclinal divisions in the first and second subsurface layers (Fig. 11, arrow). The ray flower primordium expands into a rounded protuberance (Fig. 4, arrow) by general cell division. The duration of this rounded stage seems to be
somewhat prolonged in the ray flowers, as relatively more primordia can be found in this stage on an inflorescence (Fig. 12). The apical flattening into the plug stage (Figs. 28, right; 29, right) and the subsequent development of the corolla ring meristem (Figs. 28, left; 30, RM) occur rapidly; flat-topped plug stages may be located but are few compared to the number of flowers in the ring corolla stage (Figs. 12, 28)

The corolla in the form of a ring meristem (Figs. 28-31, 33) is the first structure to appear, after which the floral apex is concave. The corolla is cylindrical at this stage (Fig. 30). Ray flowers of *E. philadelphicus* fail to develop distinct corolla lobe primordia on the corolla ring meristem, nor are any teeth, lobes, or notches seen in later stages of ray flower development (Figs. 2, 14, 40). The limb of the ray flower develops an evenly rounded apex which is retained throughout development. Differential expansion of the corolla ring meristem begins with abaxial enlargement (Figs. 36, 37) as the first indication of bilateral symmetry. The adaxial portion of the corolla can be seen during early ontogeny (Figs. 36-39, arrows), but does not expand after the corolla ring meristem stage. The abaxial portion of the corolla ring meristem develops as a blade by expanding (Figs. 36, 37), and then elongating, and curving upward (Figs. 14, 39-41).

While the corolla is still in the ring meristem stage, the pappus ring meristem is formed (Figs. 30, arrow; 32) encircling the ray flower just below the corolla ring meristem. Individual pappus primordia differentiate from the pappus ring meristem more or less synchronously as space permits (Figs. 34-36).

Ray flowers of *E. philadelphicus* completely lack stamens. There is no evidence morphologically or histologically of stamens at any stage in the ray flowers observed.
At about the same time as the appearance of the individual pappus primordia, two carpels are initiated (Figs. 34, 35) on the median plane of the ray flower. The carpels arise in the subsurface layers of the concave floral apex (Fig. 35) and appear to occupy the level that would be the staminal position if stamens were initiated. General cell division will cause the apices of the carpels to become appressed (Fig. 37) and then curve upward (Figs. 38, 39) along with the expanding ray corolla limb. At the stage of carpel appression, the basal ovule is initiated (Fig. 37) in the locule of the two carpels. The ovule is anatropous (Fig. 41) and has one integument. Further development of the ovule was not followed.

**DISCUSSION**

Bidirectional floral initiation (inflorescence B in Fig. 1) has not been recorded as such in the Asteraceae, although instances of nonacropetal events have been noted (Molder and Owens, 1973; Leins and Gemmeke, 1979). Generally, the studies involve species with one or two series of rays, rather than the five to eight series found in *E. philadelphicus*, making the determination of bidirectional events more difficult. Some workers have noted that ray flowers are initiated first, but then are overtaken in size and development by the younger disk flower primordia, leaving the rays to complete their development after the more accelerated disk flowers have done so (Philipson, 1946; Lawalrée, 1948; Reese and Hilger, 1984); i.e., the ray flowers develop out of the acropetal sequence on the capitulum. In a cyto-histological study of the responses of *Cosmos bipinnatus* Cav. apices to photoperiod and gibberellin A₃, Molder and Owens (1973) reported that the ray florets are the last to initiate after two series of involucral
bracts and the disk flowers. We view this as a clear example of bidirectional initiation in the tribe Heliantheae. Leins and Gemmeke (1979) showed that floral initiation of *Echinops exaltatus* Schrader inflorescences took place acropetally, but subsequent floral development occurred in a basipetal sequence. However, since the head of *Echinops* is interpreted as a secondary conglomeration of previously reduced one-flowered inflorescences (Kunze, 1969; Jeffrey, 1978; Leins and Gemmeke, 1979; Petit, 1988), we think that this phenomenon is not properly comparable to the findings of the current work.

Preliminary evidence we have obtained suggests that the developmental pathways involved in ray flower production differ from tribe to tribe. In some tribes, including the Astereae, the actinomorphic disk flowers seem to exhibit simpler developmental pathways (Merrell, 1900; Jeffrey, 1977; Harris, personal observation) that appear to be altered or elaborated by the rays. Other species exhibit ray flower primordia which at initiation are markedly distinct in morphology and symmetry from disk flower primordia (Moncur, 1981; Harris, personal observation).

Figure 42 graphically depicts relative timing of events in ray flowers compared to disk flowers in *E. philadelphicus*. As absolute time was not measurable; the figure is subjective, but is useful for comparative purposes. Ray flowers possess the same type (but not size) of primordium as the disk flower-rounded protuberances—and they are initiated in the same parastichies. The first set of organs to develop in both floral types is the corolla ring meristem. Other similarities between the two flower types include the patterns of pappus, carpel, and ovule formation. Differences exist in timing of organogeny, the overall size of the ray flowers, the lack of stamen primordia (or presence of an empty space they would have occupied).
The present study suggests that the ray flowers of *E. philadelphicus* are not directly developmentally derived from the disk flowers. While similarities in ontogeny between the two floral types exist, no transitional flowers were found at the equator of origin or elsewhere. This suggests there is not a physiological gradient involved, but that a genotypic event is responsible, similar to the system described in the ongoing work of Ford and Gottlieb (1989). Jeffrey's (1977) hypotheses of corolla form evolution in the Asteraceae are corroborated in part by the present study. In his scheme, both the actinomorphic disk flower and the reduced ray flower are derived from the ancestral bilabiate flower, with the implication that the reduced ray flower is more highly derived (i.e., has gone through more intermediate forms). Thus, ray flowers are more derived in relation to the disk flowers of *E. philadelphicus*, but may or may not be homologous and directly comparable to ray flowers in other taxa of the diverse Asteraceae.
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Fig. 1. Schematic diagrams of Asteraceae inflorescences with basal involucral bracts, three series of ray flower primordia (stippled circles) and disk flowers (solid circles). Arrows indicate order of initiation. 1A. General plan of acropetal floral initiation and development found in the Asteraceae (those species with flat rather than hemispherical capitula demonstrate centripetal initiation, homologous to the acropetal initiation illustrated here). 1B. Bidirectional floral initiation and development of *Erigeron philadelphicus*. The dotted line represents the equator of origin.
1. Erigeron philadelphicus
Plate 1. Figs. 2-4. Inflorescence axes of *E. philadelphicus*. All SEM views are oriented with the apex of the inflorescence located towards the top of the micrograph and the base towards the bottom unless otherwise noted. 2. Approximately life-size inflorescence axis of *E. philadelphicus*. Arrow indicates the terminal inflorescence at the center. 3. Inflorescence axis with two secondary inflorescence primordia (I) visible proximal to the larger terminal inflorescence and located in the axils of inflorescence bracts (B) which have been removed. 4. Median longisection of slightly older axis with disk (D) and ray (R) flower primordia on the terminal inflorescence appearing as rounded protuberances. Bars = 50 µm.
2. **Erigon philadelphicus**
Plate 2. Figs. 5-11. Inflorescence development in *E. philadelphicus*. **5, 6.** Comparable stages of inflorescence development. **5.** SEM view of "bald" inflorescence, shallow floral primordia may be noted at the equator (arrow.) **6.** Median longisection of inflorescence similarly aged to Fig 5. Increased meristematic activity may be noted by the densely staining region at the arrow. **7, 8.** Comparable stages of progressing floral initiation. **7.** SEM view of several series of disk flower primordia that have (are) initiated in acropetal sequence (D), and ray flower primordia (R) beginning to initiate in basipetal sequence. **8.** Median longisection of an inflorescence with a region (between arrows) of several periclinal divisions in the first subsurface level and more randomly oriented divisions deeper that will give rise to disk flowers. Ray flowers will be located in the band between the arrow-delimited region and the base of the involucral bract. **9-11.** Inflorescences with half of the capitulum covered with flower primordia. **9.** SEM view of the stage in which the disk flower primordia (D) are already noticeably larger than the ray flower primordia (R) which have filled the meristematic band from the equator down to the level of the uppermost involucral bracts (IB; most have been removed). The ray flower primordia stand in the same parastichies established by the disks. **10.** Median longisection of comparable stage to Fig. 9, with disk and ray flower primordia present. Ray flower primordia are not evident on the left as the section has passed through a region between parastichies. **11.** Higher magnification of boxed portion of Fig. 10 showing the demarcation between disk flower primordia (D) and ray flower primordia (R) and initiation stages of ray primordia (arrow.) Bars = 50 μm.
3. *Erigeron philadelphicus*
Plate. 3 Figs. 12-14. Later stages of inflorescence development in *E. philadelphicus*. 12. SEM view of completed floral initiation. Organogenesis of the disk flowers beginning with those primordia located at the equator and radiating upwards. The first recognizable structure to differentiate from the corolla ring meristem may be seen in the third disk primordium up from the equator in any parastichy and is the median abaxial corolla lobe (arrow labelled A.) Primordia that are second up from the equator display the next two corolla lobes to differentiate simultaneously, the lateral corolla lobes (paired arrows labelled L). The oldest and most developed disk primordia at the equator display the last two corolla lobes located adaxially (paired arrows labelled X). Ray primordia are still in the plug stage. Bar = 50 µm. 13. Polar SEM view of another inflorescence of approximately the same age with only disk flower primordia visible. Arrow indicates the terminal position that is unoccupied. Bar = 50 µm. 14. Inflorescence prior to anthesis. Ray flower corollas have expanded into ligules (R) which curve inward. Bar = 500 µm.
4. *Erigeron philadelphicus*
Plate 4. Figs. 15-22. Disk flower organogenesis in E. philadelphicus. 15, 16. Disk flower primordia in "plug" and corolla ring meristem stages. 15. Side SEM view of disk primordia, apex of the inflorescence located towards the left and the equator to the right. The corolla ring meristem (RM) is present in those primordia at the equator. 16. Median longisections of comparable stages of plug (left) and corolla ring meristem (right), both exhibiting subapical initials (arrows.) 17, 18. Corolla lobe primordia and pappus ring meristem stages. 17. SEM view of sightly damaged disk flower on right with all five corolla lobes (c) differentiated from the ring meristem corresponding roughly to primordium on the right in Fig. 16. Corolla lobes of the slightly older flower on the left are more developed and the girdling pappus ring meristem is noticeable (arrows.) 18. Median longisection of disk flower at approximately the same stage as flower on left in Fig. 17. Action of the subapical initials (arrows) has caused the expansion of the corolla lobes, and short files of derivatives may be seen in the subsurface layer. The region on the flanks of the flower that will bear the pappus ring meristem (p) displays some cell enlargement, but no divisions. 19, 20. Stamen initiation. 19. Oblique SEM view of flower at stamen initiation stage. Five stamen primordia (s) are located on the concave floral apex alternate with the corolla lobe primordia (c), and the pappus ring meristem is evident below the corolla (p.) 20. Median longisection showing a periclinal division in the first subsurface layer of stamen initiation (s) and pappus formation (p.) 21, 22 Carpel initiation and differentiation of pappus members. 21. SEM of older disk flower in which the individual pappus members (p) are evident on the pappus ring primordium. Corolla lobes (c) have expanded and arched inward and the corolla tube (t) has elongated to conceal the interior of the flower. 22. Median longisection showing initiation of the two carpels (g) and the fusion of the
corolla tube (t) and the developing stamen primordia (s.) Bars = 50 μm.
5. *Erigeron philadelphicus*
Plate 5. Figs. 23-27. Further disk flower development in E. philadelphicus. 23, 24. Carpel appression. 23. SEM with flowers removed at lower right, partial view of a single disk flower parastichy, with the flower at the lower left having larger pappus members than those above it. Higher in the parastichy, the pappus members (p) are just beginning to expand. 24. Median longisection of a comparable stage to the labelled flower in Fig. 23. Carpel apices (g) have elongated and become appressed, and the apices of the pappus members (p) are densely stained reflecting their increased meristematic activity. 25. Median longisection showing the continued elongation of the carpels (g), and the formation of the basal ovule primordium (o), in the single locule. 26. Median longisection of an older flower showing the development of the ovule (o) which is highly meristematic. 27. Nonmedian longisection of a disk flower showing the recurvation of the anatropous ovule (o), and pollen tetrads present in the anther locules (a.) Bars = 50 µm.
6. *Erigeron philadelphicus*
Plate 6. Figs. 28-35. Ray flower development in *E. philadelphicus*. 28, 29. Ray flower primordia in plug and early corolla ring meristem stages. 28. SEM view with the apex of the inflorescence to the lower left and the base to the upper right. Ray flower primordia closest to the equator, on the left, show the development of the corolla ring meristem (RM), while those located furthest from the equator on the right are still in the plug stage. 29. Median longisection of ray flower primordia in the plug stage, left, and early corolla ring meristem stage, right. 30-33. Late corolla ring meristem and pappus ring meristem stages. 30. SEM of ray flower primordia in late corolla ring meristem (RM) stage and slightly older stage above and closer to the equator in which the pappus ring meristem (p) is evident as a ridge encircling the flower below the corolla. 31. Median longisection of a ray flower primordium in midcorolla ring meristem stage corresponding to the flower labelled "RM" in Fig. 30. 32. Median longisection of a slightly older flower corresponding to the flower labelled "p" in Fig. 30 showing the initiation of the pappus (p.) 33. Cross section of a ray flower at the corolla ring meristem. 34, 35. Carpel initiation. 34. SEM view of ray flower showing carpel (g) and pappus member (p) initiation. 35. Median longisection of early carpel (g) and pappus (p) initiation. Bars = 50 μm.
7. *Erigeron philadelphicus*
Plate 7. Figs. 36-41. Continued ray flower development in *E. philadelphicus*. 36, 37. Enlargement of the abaxial portion of the corolla ring meristem. 36. SEM view with the abaxial half (b) of the corolla ring meristem starting to expand while the adaxial portion (d) has not. 37. Median longisection of the same stage showing the appression of the carpels (g), the initiation of the ovule (o), and the size differential between the abaxial (b) and adaxial (d) portions of the corolla. 38, 39. Expansion of the abaxial portion of the corolla to form the ligule. 38. SEM view of several parastichies of ray flowers below the disk flowers at the equator. Note the basipetal course of development by comparing the size of the pappus members. The abaxial portion of the corolla (b) curves upward, while the adaxial portion just visible at the tip of the arrow labelled "d" remains unchanged in size. Two carpels (g) are still visible. 39. Median longisection of similar stage showing the development and upcurving of the ovule (o) and the development of the abaxial portion of the corolla whose expansion also causes the carpels (g) to curve also. Note the relatively unchanged aspect of the adaxial portion of the corolla (d.). 40, 41. Development of the ligule and ovule. 40. SEM view of the elongating ligule (b) and pappus members (p.). 41. Nonmedian longisection of a comparable stage showing the recurvation of the anatropous ovule (o.) Bars = 50 µm.
Fig. 42. Diagram of the relative timing of ontogeny in disk flowers (upper bar) and ray flowers (lower bar) of the same age in E. philadelphicus. As it was not possible to measure the absolute timing of the ontogenetic events, the lengths of the stages are only intended to compare floret development and to graphically illustrate the marked heterochrony observed in this species.
Ontogenies

Chapter 4
INTRODUCTION

The inflorescence and floral morphologies of 39 species in approximately 12 tribes of Asteraceae were compared, using the scanning electron microscope (SEM) to document the early stages of inflorescence and flower development. Investigations of this type have proven quite useful with other families, such as legumes (Tucker, 1989), the Loasaceae (Hufford, 1988a, 1988b), and the Zingiberales (Kirchoff, 1988), particularly in elucidation of unclear taxonomic affiliations. In addition to the species of Asteraceae, four other species were examined, representing the three families that are the likely outgroup or sister families to the Asteraceae (Bremer, 1987; Jansen, 1990; Michaels and Palmer, 1990). By examining the sister taxa of the Asteraceae, the numerous developmental characters recorded in the current study can be tentatively polarized by outgroup comparison (Watrous and Wheeler, 1981). Primitive ontogenetic events may thus be distinguished from derived pathways, providing a basis for elucidation of the convoluted and complicated systematics of the Asteraceae.

Traditionally, studies of inflorescence and/or flower initiation and development have utilized sections examined with the light microscope (Philipson, 1953; Boke, 1947). While studies of this nature readily record cytological and cellular events, the technique has several overriding shortcomings, such as the excessive time required, the difficulty of extrapolation of the two-dimensional image to the three-dimensional reality, and the potential for creating artifacts during processing, to name but a few. The use of the SEM eliminates these problems in data collection, and substitutes one main drawback—that histological observations cannot be made. To prove the utility and dependability of the SEM in the current study, one species,
Erigeron philadelphicus, was examined in depth, using both techniques, Ch. 3 p. 33 This portion of the study demonstrates the reliability of the SEM in recording developmental events.

MATERIALS AND METHODS

Inflorescences of about 200 Asteraceae species were collected or otherwise acquired for the current study. Of these, 39 species were chosen for examination. The living material was obtained from field collections, plants grown from seed in the greenhouse, plants collected from several botanical gardens, or plants purchased at commercial nurseries. Several workers in addition to the author collected or donated material.

Inflorescences of all stages were fixed in formalin-acetic acid-alcohol (FAA): 90 cc 50% ethanol: 5 formalin: 5 acetic acid. Voucher specimens were collected simultaneously and are deposited in the Louisiana State University Herbarium (LSU). The preserved material was dissected and examined in 95% ethanol. Often, some of the flowers or other structures were removed to facilitate examination of the remaining structures. Specimens were then dehydrated in an alcohol/acetone series, and critical-point dried in a Denton DCP-1. Specimens were mounted on SEM stubs and coated with gold-palladium in a Hummer II sputter-coater.

The prepared floral material was studied with a Hitachi S-500 SEM at 25 kV, and representative micrographs were taken. For each species examined with the SEM, 50 to 150 micrographs were taken of all the available stages of development of the inflorescence and the flowers. Over 3,000 micrographs were taken in the course of the study. Representative micrographs were chosen for the following
plates to depict as many developmental stages as possible. Within a species, variation in inflorescence and floral ontogenies between heads or individuals was found to be minimal, except for the cultivated species, *Calendula officinalis* and *Xeranthemum annuum*. These species displayed some plasticity in the number of flowers per head, and in the ratio of disk flowers to ray flowers. Although the head size and makeup varied, the ontogenies of the flowers themselves were not affected, remaining consistent within the species.

For sectioning, FAA-preserved material was dehydrated in tertiary-butyl alcohol and embedded in "Paraplast". Sections were cut 7 μm thick with a rotary microtome, mounted on slides, and stained sequentially with safranin and alcian green, modified from Joel (1983) after Rudall (pers. comm. to S. C. Tucker), for study with the light microscope.

The SEM micrographs in the plates have generally been positioned so that the apex of the inflorescence is towards the top. If another orientation was used, the direction of the apex is indicated with "A" and an arrow.

The most common abbreviations in the following plates are:

- l--involucral bracts (bracts)
- RB or B--receptacular bracts (palea)
- D--disk flower
- R--ray flower
- S--stamen
- G--carpel
- C--corolla lobe
- CT--corolla tube
- P--pappus
- O--receptacular outgrowth
- RM or M--ring meristem (either corolla or pappus as indicated)
A, with arrow--indicates direction of inflorescence apex
Table 4.1. *Species examined in the study.*

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<tr>
<th>Tribe: species</th>
<th>Collector #</th>
<th>location</th>
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<tr>
<td><strong>Subfamily Asteroideae</strong></td>
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<tr>
<td><strong>Anthemideae:</strong></td>
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<tr>
<td><em>Anthemis cotula</em> L.</td>
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<td><em>Erigeron philadelphicus</em> L.</td>
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<td><em>Chrysanthemoides monilifera</em> (L.) T. Norl.</td>
<td>JRA s.n.</td>
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<tr>
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<td>Holmes Co. FLA</td>
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<td><em>Liatris pycnostachya</em> Michx.</td>
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<tr>
<td><strong>Heliantheae, sensu lato:</strong></td>
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<tr>
<td><em>Dyssodia tenuiloba</em> (DC.) B. L. Robinson.</td>
<td>EMH 604</td>
<td>Grnhs orig. from central and S. America</td>
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<td><em>Eclipta alba</em> (L.) Hassk.</td>
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<td>Allen Par., LA</td>
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<td><em>Galinsoga parviflora</em> Cav.</td>
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<td>Rudbeckia laciniata L</td>
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<td>W. Felic. Par., LA</td>
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<td>Tithonia rotundifolia Blake.</td>
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**Inuleae:**

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<td>Pluchea foetida (L.) DC.</td>
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**Senecionae:**

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<td>Tang. Par., LA</td>
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<td>Gynura sarmentosa DC.</td>
<td>EMH 939</td>
<td>MO Bot. Gdn, MO</td>
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<tr>
<td>Senecio glabellus Poiret</td>
<td>EMH 123</td>
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**Subfamily Cichorioideae**

**Arctoteae:**

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<tr>
<td>Venidium fastuosum Stapf.***</td>
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**Cynareae:**

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<td>Centaurea maculosa L.</td>
<td>EMH 395</td>
<td>Rockbridge Co., VA</td>
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<td>Xeranthemum annum L.</td>
<td>EMH 605</td>
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<td><em>Acoptia runcinata</em> (D. Don) B. L. Turner</td>
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<td><em>Mutisia coccinea</em></td>
<td>EMH 1039 living collection orig. SE Brazil</td>
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<td><em>Trixis chiapensis</em> C. Anderson</td>
<td>EMH 1032 Chiapas, Mexico</td>
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<tr>
<td><em>Trixis inula</em> Crantz*</td>
<td>AWL 2399 Veracruz, Mexico</td>
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<td><strong>Vernonieae:</strong></td>
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<tr>
<td><em>Calycera herbacea</em> Cav.***</td>
<td>MLD 1206 Laguna de Manle, Chile</td>
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<td></td>
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<tr>
<td><em>Calycera leucanthema</em> (Poepp. ex Less.) O. Ktze.</td>
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Table 4.1. continued

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<td><strong>Goodeniaceae</strong></td>
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<tr>
<td><em>Scaevola calendulacea</em> (Andr.) Druce</td>
<td>SCT 28892 Davis, CA</td>
<td>cultivated, orig. Australia</td>
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</tbody>
</table>

* = missing one intermediate stage.

** = a cultivar deemed too variable for consistent inflorescence ontogeny, but with useful floral development stages.

*** = missing several important stages.

Collectors:

Botanical Gardens:

Longwood Gardens, Kennett Square, PA
Missouri Botanical Garden, St. Louis, MO
U. C. Berkeley Botanical Gardens, Berkeley, CA
Royal Botanical Gardens at Kew, Surrey, Great Britain
Rancho Santa Ana Botanical Gardens, Claremont, CA
Tribe: Anthemideae

The Anthemideae were traditionally divided into two subtribes (Lessing, 1836) based on the presence of receptacular bracts. This was recognized as a poor character for tribal subdivision (Bentham, 1873a). Currently, the subtribal delimitations of the Anthemideae are in flux, pending a better understanding of the genera in the tribe (Heywood and Humphries, 1977). Seven provisional groups were established by Reitbrecht (1974). Of those groups, Anthemis cotula, of the "Matricaria-gruppe", and Artemisia pycnocephala, of the "Artemisia-gruppe", were examined.
**Anthemis cotula** L.

"Dogfennel", collected from a disturbed site on the Mississippi River levee, in Baton Rouge, Louisiana.

Organogenesis sequence: Disk: Co, S, G  Ray: Co, (S)/G

Scale: Bars in Figures 1-4, 7-10, 12, and 13-16 = 50 μm
Bars in Figures 5, 6, 11, and 17 = 500 μm

Dogfennel is a stout, taprooted herb that grows in waste places. The plant has numerous branches with terminal heads. Numerous heads may be flowering concurrently on a vigorous individual. There are about 80-100 yellow disk flowers and 16 white ray flowers per head.

**Inflorescence**--The inflorescence meristem is almost spherical (Fig. 1) as floral initiation begins. The disk flower primordia are the first to arise (Fig. 1, arrowheads labelled D) acropetally in parastichies. At the base of each parastichy, a roughly triangular area remains uncommitted (Fig. 1, arrowheads labelled R). The ray flower primordia are initiated (Fig. 2, arrowheads labelled R) after several series disk flower primordia have initiated and enlarged (D in Fig. 2). As floral initiation progresses on the head, organogenesis begins in the lowermost disk flower primordia (D in Fig. 3), while the rays
8. Anthemis cotula
are suppressed in development (Figs. 3 and 4, arrowheads labelled R). Not until almost all of the disk flowers on the head have undergone organogenesis (Fig. 5) do the ray flowers begin to differentiate (Fig. 5, arrowheads labelled R). In later stages of development, the ray flowers elongate (Fig. 6, arrowheads labelled R). The lowermost disk flowers also elongate occasionally (Fig. 6, arrowheads labelled D), and become incurved like the rays.

**Disk flower**--The disk flower primordia are initiated as rounded protuberances (P, upper part of Fig. 7). The outermost disk flowers are subtended by receptacular bracts; both are initiated together as a common primordium (not shown). As the disk flower primordia enlarge into the plug stage (P in Fig. 7), the receptacular bract is obscured (but shown in Fig. 8, B). The corolla ring meristem appears soon (M in Fig. 7), giving rise simultaneously to five corolla lobe primordia in short order (C in Fig. 8). Five stamen primordia are then initiated more or less simultaneously on the concave sides of the floral apex (S in Fig. 9). Two carpel primordia are initiated next (G in Fig. 10) on the radial plane of the head after the corolla lobes have arched inward. As the corolla tube elongates, numerous multicellular glandular trichomes develop (Figs. 11 and 12, arrowheads labelled T). No pappus was seen in this species.

**Ray flower**--The ray flower primordia are initiated at the base of each disk flower parastichy (Fig. 13, at arrowheads labelled R); these ray primordia are smaller in diameter than similarly aged disk flower primordia. As the disk flowers progress through organogenesis, the ray flower primordia slowly enlarge to the plug stage (P in Fig. 14) and then develop an irregular ring meristem (M in Fig. 15). The lateral and
9. Anthemis cotula
abaxial portions of the corolla enlarge equilaterally (Fig. 16), and the adaxial portion is suppressed. Simultaneously, two carpel and two stamen primordia are initiated (G and S in Fig. 16), but are soon aborted to produce a neuter flower at maturity. By anthesis (Fig. 17) a short corolla tube has been produced by zonal growth (CT). The mature ray flower lacks apical teeth on the ligule, and lacks any manifestation of a pappus.
10. *Anthemis cotula*
Artemisia pycnocephala DC.

"Wormwood", obtained from the collection of the Rancho Santa Ana Botanical Gardens in Claremont, California. The species is a coastal one, ranging from Monterey County, California, to Oregon.

Organogenesis sequence: Disk: Co, S, G Ray: Co, (S)/G

Scale: Bars in Figures 1-4, 7-11, 12, and 13-18 = 50 μm
Bars in Figures 5, 6, 12, 19, and 20 = 500 μm

Wormwood is low trailing perennial with heads arranged in terminal racemose synflorescences. There are about 15 disk flowers and 8 small ray flowers per head.

Inflorescence--The inflorescence meristem has a hemispherical dome shape (Fig. 1) prior to floral initiation. Disk flowers are the first to initiate (D in Fig. 2) as low mounds around the base. The ray flower primordia occupy the remaining uncommitted areas around the base of the inflorescence meristem (R in Figs. 2 and 3) and are slightly irregular in outline (R in Fig. 3). Organogenesis begins with the disk flowers and proceeds acropetally on the head (D in Fig. 4). The ray flower primordia lag behind the disk flowers in stage of development (R in Fig. 4); only catching up in size
11. Artemisia pycnocephala
during the later stages of development (Figs. 5 and 6 arrowheads labelled R). Just prior to anthesis (Fig. 6) the receptacle still retains the original hemispheric shape.

**Disk flower**—After their initiation (D in Fig. 2), the disk flower primordia soon enlarge to rounded protuberances (Fig. 7) and then the plug stage (P in Fig. 8). A corolla ring meristem develops apically almost immediately (M in Fig. 8) as the first sign of organogenesis. Five corolla lobe primordia differentiate from the corolla ring meristem simultaneously (C in Fig. 9). Stamens are the next to arise, also simultaneously; and are located on the interior of the concave floral apex, alternate with the corolla lobes (Fig. 9, arrowhead). The corolla lobes expand and arch inward to cover the interior of the flower (Fig. 11), after which, the two carpel primordia are initiated (G in Fig. 10, same flower as in Fig. 11). Just before anthesis (Fig. 12), the stamens have fully differentiated (S). The achene is almost obsolete (arrowhead labelled A), and the stigma (St) is not functional, as seen by the presence of a truncate tip rather than two stigmatic branches. The disk flowers are thus male in function.

**Ray flower**—The initially irregular ray flower primordium (R in Fig. 13) soon enlarges to a plug stage (R in Fig. 3). The first organ to arise is the corolla ring meristem (M in Fig. 14). By zonal growth, the corolla elongates evenly (Figs. 15 and 16, arrowheads) for a time. After a certain length is achieved, three corolla lobes differentiate at the tip of the corolla tube (Figs. 17 and 18, arrowheads labelled C) and the numerous glandular trichomes begin to differentiate (Figs. 17-19, arrowheads labelled T). At about this time, the two carpel primordia are initiated (not shown). The corolla tube continues to elongate (CT in Fig. 19) and is essentially tubular
12. *Artemisia pycnocephala*
13. Artemisia pycnocephala
at anthesis (Fig. 20). The two stigmatic branches protrude from the corolla tube (Fig. 20, arrowheads labelled St).
While the Astereae comprise a natural grouping, subtribal delimitations are obscure due to many overlapping character states and a continuum of transitional genera between currently recognized subtribal groupings. Six subtribes have been recognized historically (Bentham, 1873; Hoffmann, 1894), but the dearth of consistent, strong characters distributed meaningfully throughout the Astereae led Grau (1977) to avoid updating and legitimizing any subtribal groupings in the Astereae. Lane (pers. comm.) recognizes two main lines in the Astereae: those taxa with chromosome numbers that are generally x=9, and those genera with chromosome numbers generally fewer than x=9. I have selected *Erigeron philadelphicus* to represent the x=9 line. *Erigeron* is also one of the few more or less cosmopolitan genera in the tribe. A detailed account of the ontogeny of *Erigeron philadelphicus* is found in Chapter 3, p. 33. In this study, *Chrysopsis camporum* represents the line of lower chromosome numbers, generally fewer than x=9.
Chrysopsis camporum Greene

"Golden aster" collected from a disturbed roadside site in Jefferson County, Tennessee.


Scale: Bars in Figures 1 and 7-20 = 50 µm

Bars in Figures 2-6 and 21 = 500 µm

The numerous heads in this perennial species are terminal on the many branches and form a more or less corymbiform synflorescence. All heads on the plant are roughly of the same size. Disk flowers usually number about 140 and there are 21-34 rays in a single series.

Inflorescence--The inflorescence apical meristem is first distinguishable in this species when the phyllotactic fraction increases during the transition from leaf to initiation of involucral bracts (I in Fig. 1). As the fraction continues to increase, the inflorescence apex broadens and begins to flatten (Fig. 2). The first disk flower primordia are seen (arrowheads in Figure 2) just beginning to protrude at the periphery of the otherwise uncommitted apex. Disk flower primordia (arrowheads labelled D, Fig. 3) initiate acropetally on the inflorescence apex while the ray flower primordia (arrowheads...
14. Chrysopsis camporum
labelled R) lag behind in size and shape. Organogenesis begins with the outermost disk flowers and proceeds acropetally over the inflorescence, while the ray flower primordia (Fig. 4, arrowheads) are suppressed at an early developmental stage. The ray flowers eventually begin to catch up (Fig. 5), after organogenesis on the entire capitulum has been completed, and general growth and differentiation of the flowers has begun. At this stage, some outgrowths of the receptacle become evident, scattered randomly between disk flowers (Fig. 5, arrowheads). These enation-like outgrowths arise from the surface of the receptacle in the interstices between flowers and do not directly subtend the closest flower in a strict 1:1 relationship. During late development, the outgrowths elongate (Figs. 6, 12, arrowheads) to form narrow pales. By this time, the receptacle has enlarged and become essentially flat, and will remain so through anthesis.

**Disk flower**--Development of the disk flowers in *Chrysopsis camorum* takes place much like that in *Erigeron philadelphicus*, p. 33. Disk flower primordia are initiated as rounded protrusions (D in Fig. 7) which soon enlarge into the plug stage (Fig. 8, right) and develop a ring meristem apically (Fig. 8, left). The five corolla lobe primordia become evident next (C in Fig. 9), arising simultaneously from the ring meristem. Unlike *Erigeron*, the pappus ring meristem is the next to initiate (Fig. 9, arrowhead labelled P at upper right flower), shortly before the stamens. Alternate with the enlarging corolla lobe primordia, the stamens are initiated next, appearing simultaneously (Fig. 10, arrowheads labelled S). The individual pappus members begin to differentiate at this time as bulges along the pappus ring meristem (Fig. 10, arrowheads labelled P). In Figure 11, the two carpels (G) have initiated. (The corolla and three stamen primordia have been removed.) Note the enlarged pappus primordia. During the
middle stages of development, the style elongates (flower on left in Fig. 12) and the corolla tube is formed by zonal growth (CT in Figs. 11, 12). The sequential order of development among disk flowers is evident on the capitulum at each stage of development (Figs. 3-5).

**Ray flower**—Only one series of ray flowers is formed in *Chrysopsis camporum*. The initial triangular shape of the primordium (Fig. 13, arrowheads) is quite different from that of the round disk primordia, and different from the round ray flower primordia of *Erigeron philadelphicus*. The triangular shape of the ray flower primordium is retained until organogenesis is almost complete (Figs. 13-17) but in other respects resembles the disk flower developmental sequence fairly closely. Figure 14 shows the triangular plug stage (arrowheads). An irregular corolla ring meristem forms after some elongation of the primordium, and can be seen in Figures 15 and 16. The pappus ring meristem appears next (Fig. 17, arrowheads). Four stamens are initiated in each ray flower (Fig. 18, arrowheads labelled S), which is not the case with *E. philadelphicus*. The stamens are evident during early stages of development (Figs. 18-20, arrowheads labelled S), but are aborted and resorbed (not shown) by mid-development (Fig. 21) and absent at anthesis. The individual pappus members become evident (Fig. 18, arrowheads labelled P). At the same time, the abaxial and lateral portion of the corolla ring meristem begins to enlarge (Figs. 18-20), while the adaxial portion of the corolla remains unchanged in size (Figs. 19, 20, arrowheads labelled B). As the abaxial and lateral portions of the corolla continue to elongate to form the ray flower ligule, the lack of growth on the adaxial side effectively produces the slit in the corolla tube (Fig. 21, arrowheads) along which the ligule will unroll at anthesis.
16. Chrysopsis camporum
Tribe: Calenduleae

The main center of distribution for the Calenduleae is South Africa, with a secondary center in the Mediterranean (Norlindh, 1977b, and references therein). Norlindh recognizes seven genera for the small tribe. While he has resurrected several genera submerged by other workers, no formal subtribal affiliations have been made. For this reason, I studied species from both centers of distribution. *Osteospermum fruticosum*, the largest genus of the tribe, was chosen from the South African center of distribution. *Chrysanthemoides monilifera*, also of South Africa, was also examined. *Calendula officinalis*, with a mainly Mediterranean distribution, was included in the current study, although as a cultivar, it is highly variable in head size and flower number. Rarely is a pappus initiated in this tribe, which holds true for the species examined here.
*Calendula officinalis* L.

"Pot marigold" or "Calendula", material collected from commercially obtained plants. Originally from the Mediterranean.

Organogenesis sequence: disk: Co, S, G       ray: Co, G

Scale: Bars in Figures 1-5, and 8-13 = 50 μm

Bars in Figures 6, 7, 14, and 15 = 500 μm

The cultivar of *Calendula officinalis* obtained for the study is a low, somewhat branched annual herb. At any one time, five to ten heads are present on a plant, solitary at the termini of the branches, with more heads constantly differentiating once flowering has begun. The size of the heads, overall number of flowers, and ratio of rays to disks was found to be extremely variable from head to head of the same plant.

Inflorescence--The flowers are initiated in acropetal sequence (Figs. 1, 6, 7 and 8), with the peripheral ray flower primordia being the first (Fig. 8). The ray flowers are aligned in orderly parastichies (Figs. 7, 14, 15), with a variable number of ray primordia ranging from three in a series or vertical row (Figs. 6) to seven (Fig. 15, arrow). At some point during floral initiation, there is a transition to disk flower
17. Calendula officinalis
primordia (D in Fig. 1) with no intermediate forms. The disk flower primordia are enlarge quickly and outstrip the older ray flower primordia in size (Fig. 6). Occasionally, some ray flowers are initiated above or among the disks after the transition to disk flowers is made (Fig. 14, arrowheads labelled R). This phenomenon is a common one noted for cultivated Asteraceae species such as Helianthus (Fick, 1976) and Chrysanthemum (Bush et al., 1976). Organogenesis occurs first in the lowermost disk flower primordia (D in Figs. 2, 9) and then proceeds acropetally on the head in the remaining disk flower primordia. Organogenesis seems to proceed rather slowly compared to other Asteraceae, in that one horizontal series of disk flowers progress past the stamen initiation stage before the next higher series of disk flowers begins organogenesis. The sequence of organogenesis and development for the ray flowers is more difficult to determine, but is generally not acropetal (Fig. 10). It appears to be somewhat synchronized (Figs. 6, 7, 10, 11) with slightly larger and more advanced flowers at mid-level in the series of rays (Figs. 10, 11, arrowheads).

**Disk flower**--Disk flower primordia are initiated as low mounds (D in Figs. 1, 6) that rapidly broaden and undergo organogenesis (Fig. 2). The corolla lobes appear first, in rapid succession (Fig. 2, numbered primordia) in a non helical, irregular order. Rapidly thereafter, the stamens (S in Fig. 2) are initiated in the same fashion. By the time the corolla lobes have expanded and covered the interior of the flower, the stamen primordia have become equalized (Fig. 3). Somewhat later, the two carpels have formed and begun to elongate apically (G in Fig. 4), retaining the original cleft which separated them as initials (Fig. 4, arrowheads). No pappus is initiated in this species.
18. *Calendula officinalis*
Ray flower—Ray flower primordia are initiated in an acropetal order (R in Fig. 8), mostly as low, rounded mounds with some of lowermost primordia somewhat distorted in shape. The two lateral corolla lobe primordia are initiated first (Fig. 9, adaxial view, arrowheads), rapidly followed by the abaxial and adaxial corolla lobe primordia (Figs. 10, 11, numbered primordia). After its initiation, the adaxial corolla lobe primordium is immediately suppressed (Fig. 13, arrowheads), so that the elongating corolla is essentially trimerous (Figs. 14, 15), and three-toothed at anthesis (not shown). Stamen primordia were not seen in any of the ray flowers examined. Last to initiate are the two radially oriented carpels (Figs. 12 and 13, arrowheads labelled G).
Chrysanthemoides monilifera (L.) T. Norl.

"Chrysanthemoides", material obtained from the collection of Longwood Gardens in Kennett Square, PA. Originally from South Africa.

Organogenesis sequence: disk: Co, S, G  ray: Co, S, G

Scale: Bars in Figures 1, 2, 7-11, and 13-17 = 50 μm

Bars in Figures 3-6, 12, 18, and 19 = 500 μm

This woody perennial often attains the height of three to four meters and is in the form of either a profusely branched small tree or a large sprawling shrub. Heads are terminally located in a corymb-like arrangement. Ninety to 120 yellow disk flowers and a single series of 10-16 white ray flowers are present on each head. In this species, the disk flowers are functionally male. While carpels and styles are produced by the disk flowers, the ovaries do not develop. The ray flowers are fertile, and produce fruits in the form of fleshy drupes; this fruit type is quite unusual for this family.

Inflorescence--The bare inflorescence meristem has a hemispherical shape (Fig. 1), retained until mid-development (Fig. 5). Disk flower primordia (D in Fig. 2) initiate acropetally as rounded protuberances. After a time lag, the single series
19. Chrysanthemoides monilifera
of ray flower primordia is initiated basally; they are somewhat compressed or distorted in outline (D, R in Fig. 2). Organogenesis on the head begins with the outermost disk flower primordia (Fig. 3) before all disk flower primordia have initiated. The first organs are the corolla lobes which quickly expand (Fig. 3, arrowheads) and overlap other primordia that are less developed. Organogenesis in a flower primordium proceeds to the stage of stamen initiation (Fig. 4, arrowhead) before the adjacent but higher disk flowers show any evidence of organogenesis. After two or three series of disk flowers have differentiated, the ray flowers undergo organogenesis as well (Fig. 4, arrowheads labelled R). Floral initiation on the inflorescence meristem has been completed at this stage (Fig. 4). As organogenesis and subsequent development is completed for all flowers on the head, (Fig. 5) the receptacle broadens and flattens. Ray flowers are still smaller than the neighboring disk flowers (D in Fig. 5, arrowheads labelled R). Mid-way through development, the rays have caught up to the disk flowers in size (D, R in Fig. 6).

**Disk flower**—The primordia of the disk flowers arise on the surface of the inflorescence meristem as rounded protuberances without any subtending receptacular bracts (Fig. 7). The corolla lobes form in quick succession on each flower (Fig. 8, arrowheads) somewhat limited by the available space. Initiation is presumed to be sequential rather than simultaneous, as corolla lobes are initially of slightly different sizes (Figs. 8, 9). Stamens are initiated next, in a rapid sequence (Fig. 9, arrowheads). Last to initiate are the two carpels seen in the dissected flower in Figure 10 (arrowheads labelled G). The carpels elongate apically (Fig. 11, flower on left, arrowhead). Just before anthesis (Fig. 12), the achene is relatively undeveloped (lower left).
20. Chrysanthemoides monilifera
Ray flower--Ray flower primordia are initiated (Fig. 13, arrowheads) from triangular regions around the base of the inflorescence meristem in areas delimited by the initiation of the disk flower primordia. The primordia enlarge into a plug stage (Fig. 14, arrowheads), and still show a triangular or trapezoidal outline. As the disk flower primordia begin organogenesis, the ray flower primordia are somewhat obscured by the corollas of the more advanced disk flowers (Fig. 3). The corolla lobes of the ray flowers are initiated (Fig. 15) following a roughly pentameric pattern although lobes may be unequal (Fig. 15). Stamen primordia are initiated and are evident on the concave sides of the floral meristem (Fig. 15, arrowheads). Four or five stamen primordia are produced in sequence alternate with the corolla lobe primordia. These become staminodia. Two carpels are initiated in a radial row (G in Fig. 11) as the two lateral and abaxial corolla lobes elongate zonally (Fig. 16, flower same age as lower right in Fig. 11). The staminodia remain evident (Figs. 11, 17, arrowheads labelled S) until anthesis (Fig. 19). The achene begins to enlarge at the stage of carpel initiation (Fig. 16) and continues to enlarge as the two stigmatic branches elongate (Fig. 17, same age flowers as in Fig. 18). In Figure 19, at anthesis, the paired stigmatic lines on the outer edges of the branches can be seen (arrowheads).
21. Chrysanthemoides monilifera
Osteospermum fruticosum (L.) T. Norl.

"Osteospermum", material collected from cultivated specimens in Monterey County, CA. Originally from South Africa.

Organogenesis sequence: disk: Co, S, G       ray: Co, S, G

Scale: Bars in Figures 1-3, 7-11, and 13-20 = 50 μm

Bars in Figures 4-6, 12, 18, and 21 = 500 μm

This species sprawls to produce a ground cover with interesting foliage and attractive purple and white inflorescences. Heads are borne singly on axillary scapes. About 100 disk flowers and a single series of 18-28 ray flowers are present on each head. At anthesis, the disk flowers are purple with bright orange stamens and stigmas, and the ray corollas are whitish with purple veins above and solid purple below.

Inflorescence--The inflorescence meristem of O. fruticosum is initially hemispheric (Fig. 1) as it differentiates from a vegetative state. By the time flower primordia appear, the inflorescence attains the conical shape typical of the tribe (Fig. 2). Disk flower primordia are first initiated at the base of the inflorescence meristem (D in Fig. 2). Subsequent disk primordia are initiated acropetally and appear to be arranged in parastichies (Fig. 2, arrows). Ray flower primordia are
22. Osteospernum fruticosum
somewhat delayed in their initiation (R in Fig. 2) until two or so disk flower primordia are already apparent above. The ray flower primordia are located at the base of each parastichy formed by the disk flower primordia. The lowermost disk flower primordia are the first to begin organogenesis (Fig. 3), which then proceeds acropetally on the head. The ray flower primordia lag behind the disks only briefly before they (the rays) also start organogenesis (Figs. 3, 4). As organogenesis proceeds on the head, the oldest disk flowers progress to stamen and carpel initiation before organogenesis has even begun in the youngest disk flower primordia located apically (Fig. 4). The disk flowers become more equalized in size and developmental stage (Figs. 5, 6). The conical shape of the receptacle is retained through late development (Fig. 6) when the flower are undergoing final corolla expansion prior to anthesis.

**Disk flower**—Disk flower primordia arise as low mounds (Fig. 2) and then expand rapidly into the plug stage (Fig. 7). The corolla lobe primordia arise quickly but sequentially, with the abaxial lobe usually appearing first (Fig. 8, numbered "1"). The lateral lobe primordia are the next to arise in a sequential fashion ("2" and "3"), with the two abaxial lobe primordia appearing last ("4" and "5"). Soon after the corolla lobes have begun to expand and arch inward (Fig. 9), the stamen primordia are initiated (Fig. 8, flower of the same age as in Fig. 9, arrowheads), also sequentially, and alternate with the corolla lobes. Although an encircling ridge becomes evident (Fig. 10, arrowheads) girdling the disk flower midway, a pappus is not produced (Fig. 12). The ridge is thus interpreted as the upper "shoulder" of the achene that is delimited when the corolla tube starts to elongate by zonal growth (Fig. 10, arrowheads labelled CT). At the same time, two carpel primordia are initiated (Fig. 11, dissected flower the same age as in Fig. 10,
23. Osteospermum fruticosum
carpels at arrowheads labelled G). By mid-development, the corolla lobes and tube have elongated (C, CT in Fig. 12) and trichomes have differentiated on the base of the corolla tube.

Ray flower--The primordia of the ray flowers (Fig. 13, arrowheads) begin as rather irregularly shaped mounds at the base of each parastichy of disk flowers. They expand into the plug stage (Fig. 14, arrowheads), and begin organogenesis only shortly after neighboring disk flower primordia (compare D, R in Fig. 15). The lateral corolla lobe primordia are the first to appear (Fig. 15) followed by the abaxial and adaxial lobes (Fig. 16). The adaxial lobe is immediately suppressed (Figs. 18, 19, arrowheads), so that the zonal growth of the three remaining lobes form the ligule of the ray flower (Fig. 21, 3 apical lobes still apparent, arrowheads). Four stamen primordia are initiated (S in Fig. 17). In Figure 17, two of the four stamen primordia on the left have been dissected away. Almost immediately thereafter, the two carpel primordia are initiated (Fig. 17, arrowheads labelled G) as elongated swellings separated by a groove. The stamen primordia enlarge somewhat (Figs. 19, 20, arrowheads labelled S), but are soon suppressed and the elongating style overtakes them in size (Fig. 20, arrowheads labelled G). Dissected mature ray flowers (not shown) often show small relictual staminodia in the corolla tube. By late development, there are numerous trichomes on the base of the corolla tube (Fig. 21, arrowheads labelled T) which should not be confused with a bristle-like pappus.
24. Osteospermum fruticosum
In the most recent treatment of the Eupatorieae, King and Robinson (1987) divided the tribe into 18 subtribes, several of which contain relatively few genera. I chose to examine *Eupatorium fistulosum* of the subtribe Eupatoriinae, and *Liatris pycnostachya* of the subtribe Liatrinae.
Eupatorium fistulosum Barratt

"Joe-Pye weed", collected roadside in Holmes County, Florida.

Organogenesis sequence: Co, P, S, G

Scale: Bars in Figures 1-5, and 7-12 = 50 μm
Bar in Figure 6 = 500 μm

Joe-Pye weed is a robust perennial herb with a rarely branched main axis. The heads are terminal and arranged in paniculiform synflorescences which are terminal on the main axis. The heads are discoid, with 5-10 flowers each.

Inflorescence--The inflorescence meristem is a low-domed hemisphere (Fig. 1). Flower initiation is quickly completed (F in Fig. 2) as relatively few flower primordia are produced on the receptacle in this species. After the flowers have initiated and enlarged (Fig. 3), occasional receptacular bracts initiate, usually in a subtending position to individual flowers (Fig. 3, arrowheads labelled B). Organogenesis begins with the outermost flowers (Fig. 4, arrowheads), and proceeds centripetally (Fig. 5). Prior to anthesis (Fig. 6), all the flowers are essentially equalized in stage and size.
25. Eupatorium fistulosum
Flower--The floral primordia are initiated as low mounds (Fig. 2), and rapidly enlarge to the plug stage (P in Fig. 7). A corolla ring meristem differentiates on the apex of the flower (M in Fig. 8) which gives rise to five corolla lobes simultaneously (C in Figs. 8 and 9). The pappus is the next organ of organs to initiate, becoming noticeable as bulges around the middle of the flower (Fig. 9, arrowheads labelled P). As the first five pappus members differentiate alternipetally (P in Fig. 10), five stamens are initiated simultaneously (S in Fig. 10, one pappus member obscured by bract, B). Two carpels are initiated (Fig. 11, arrowheads labelled G), after the corolla lobes have arched inward and the corolla tube has begun to elongate by zonal growth (C and CT in Fig. 12, same age as 11). Numerous short trichomes are formed on the corolla and achene as the flowers differentiate (Figs. 6 and 13, arrowheads labelled T).
26. *Eupatorium fistulosum*
Liatris pycnostachya Michx.

"Blazing star", collected roadside in a sandy area in Jefferson Davis Parish, Louisiana.

Organogenesis sequence: Co, P, S, G

Scale: Bars in Figures 1-5, and 8-11 = 50 μm
      Bars in Figures 6, 7 and 12 = 500 μm

Blazing star is a very attractive unbranched plant with the main axis arising from a basal rosette of leaves. The heads are sessile on the axis in a spicate synflorescence, and anthesis of the heads proceeds basipetally on the axis. The heads are discoid with five to ten rose to purple flowers each.

Inflorescence--The inflorescence meristem has a domed shape initially (Fig. 1). The five to eight disk flowers are initiated more or less simultaneously around the periphery of the inflorescence meristem (Fig. 2). Organogenesis on the head also takes place simultaneously (Figs. 3-6). There seems to be some crowding effect due to the pressure of the involucral bracts; as the pappus primordia are being initiated, those that are located on abaxially are temporarily suppressed (Fig. 5, arrowhead). The effect is short-lived, however, and all the
27. Liatris pycnostachya
pappus members eventually attain the same length (Figs. 7, 12).

*Flower*--The floral primordia quickly enlarge to the peg stage (Fig. 2) after they are initiated. A corolla ring meristem is seen briefly (M in Fig. 8). Five corolla lobes are differentiated more or less simultaneously (C in Fig. 8). The pappus primordia are the next to appear; the first members alternate with the corolla lobes (Fig. 9, arrowheads), except for the abaxial site as noted above. Additional pappus primordia fill in the gaps (Figs. 5 and 10), with the abaxial side remaining unoccupied until the other pappus members have elongated (Fig. 6). As the corolla lobes arch inward (C in Fig. 10), the stamens (Fig. 10, arrowheads labelled S) are initiated in the interior of the flower, simultaneously and alternate with the corolla lobes. Two carpels are initiated (Fig. 11, arrowheads labelled G) as the other organs enlarge. At maturity (Fig. 12), the achene and pappus are covered with fine short trichomes.
28. Liatris pycnostachya
Tribe: Heliantheae

Tribal limitations of the Heliantheae have differed markedly in the treatments by several authors both in recent times, (Stuessy, 1977; Turner and Powell, 1977; Robinson, 1981; Bremer, 1987), and in the earlier literature (Cassini, 1829; Lessing, 1832; De Candolle, 1836; Bentham 1873). Some authors erect the tribes Tageteae (Cassini, 1829; Strother, 1977) and Coreopsideae (Turner and Powell, 1977) out of the Heliantheae. The paraphyletic tribe Helenieae, as conceived by Bentham (1873), has been redistributed among all of the previously mentioned taxa (Turner and Powell, 1977). In the current study, the tribe Heliantheae was approached in the broad sense with species chosen from the following taxa of the Heliantheae sensu lato:

<table>
<thead>
<tr>
<th>Species</th>
<th>Tribe</th>
<th>Group#</th>
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<td>Dyssodia tenuiloba</td>
<td>Tageteae</td>
<td>-</td>
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<tr>
<td>Eclipta alba</td>
<td>Heliantheae sensu stricto</td>
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<td>Hymenopappus artemisiaefolius</td>
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<td>Madia elegans</td>
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<tr>
<td>Tithonia rotundifolia</td>
<td>Heliantheae sensu stricto</td>
<td>1</td>
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</table>
**Coreopsis tinctoria** Nutt.

"Tickseed", collected from a disturbed site in East Baton Rouge Parish, Louisiana.

Organogenesis sequence: Disk-Co, S, G Ray-Co, S

Scale: Bars in Figures 1-4, 7-12, and 14-21 = 50 μm

Bars in Figures 5, 6, 13, and 22 = 500 μm

Tickseed is an annual herb that favors disturbed sites. Vigorous plants are much branched with 20-40 terminal heads per plant at any one time. There are usually about 160 tetramerous disk flowers and eight showy ray flowers per head. None of the flowers examined for the present study exhibited a pappus, although flowers of the species exhibit occasional a small or obsolete pappus (Cronquist, 1980).

**Inflorescence**—The inflorescence meristem has a rounded conical shape as floral initiation begins (Fig. 1). The common primordia that bifurcate to form the disk flower and receptacular bract primordia are apparent first (Fig. 1, arrowheads labelled D), at the lower edge of the uncommitted meristem. The initiation of the disk flower primordia then proceeds acropetally in orderly parastichies (Figs. 2, 3, arrows labelled D). The primordia of the ray flowers are delimited in
29. Coreopsis tinctoria
small irregular areas of meristem which remain uncommitted temporarily at the base of each parastichy (Fig. 1, arrowheads labelled R). Additionally, the ray primordia are delayed in early development (Fig. 2, arrowheads labelled R), until fairly late during differentiation when ray ligules expand (R in Fig. 6). The disk/bract common primordia are initiated until the inflorescence meristem is completely utilized (Fig. 4), by which time the lowermost disk flowers have initiated organogenesis. The sequence of organogenesis follows the acropetal pattern of initiation on the head, and takes place rapidly (Fig. 5). After bifurcation, the receptacular bract primordia (Figs. 3, 4, arrowheads labelled B) are suppressed in growth, and are surpassed in size (Fig. 5, arrowhead labelled B) by the disk flowers. In later stages, the receptacular bracts elongate (Fig. 6, B), exceeding the disk flowers in length.

**Disk flower**—Disk flowers are initiated as common primordia (Fig. 7, arrowheads labelled 1) with the receptacular bracts. Each common primordium rapidly bifurcates (arrowheads labelled 2) in an unequal division. The abaxial portion comprises about 1/3 of the common primordium and becomes the receptacular bract primordium. The adaxial portion gives rise to a disk flower primordium, which rapidly enlarges (Fig. 8) to obscure the developing receptacular bract. The first organs to arise on the disk flower primordia are the four corolla lobe primordia which appear simultaneously (Fig. 8), apparently without a preceding ring meristem stage. All the disk flowers are regularly tetramerous; no pentamerous or 6-merous flowers are found in this species. Next to arise are the four simultaneous stamen primordia, located alternate with the corolla lobes (Fig. 9, arrowheads labelled S). Last to initiate are the two carpels (Fig. 10, arrowheads G). In mid-development, as the stamens and style elongate (S in Fig. 11, arrowhead labelled St), a nectary initiates at the base of the
30. Coreopsis tinctoria
style (Fig. 11, arrowhead labelled N). A later stage of the basal disk nectary may be seen in Figure 12 (N), with corolla, stamens and the upper portion of the style dissected away. The bilateral flattening of the achene can be seen (Fig. 12), with two bulges (unlabelled arrowheads) that become "wings" in the mature achene (not shown). No pappus or other enations are formed on the achenes in the population under study (Fig. 13). The subtending receptacular bract often adheres to the achene (B in Fig. 13) after separation from the receptacle.

**Ray flower**—The primordia of the ray flowers occupy narrow area at the base of each parastichy on the capitulum (Fig. 14, arrowhead). The primordium expands in the available space (Fig. 15, arrowhead) and a very irregular ring meristem is formed on the summit of the ray primordium (Fig. 16, arrowhead). During early development, the ray primordia enlarge evenly by the ring meristem activity and zonal growth (Figs. 17, 18). Individual corolla lobes are not differentiated, and there are no distinct apical teeth on the mature ray corolla. Eventually the abaxial portion exceeds the adaxial portion (Fig. 20, arrowheads labelled Ad and Ab) and the ray corolla curves upwards. All the rays are neutral at maturity, although four stamen primordia are initiated (S in Fig. 19, flower same age as in Fig. 20). The stamen primordia do not develop any further and are eventually resorbed (Fig. 21, flower same age as in Fig. 22). Carpel primordia were not seen in any of the rays dissected. In later stages, the abaxial portion of the corolla expands and trichomes develop (Fig. 22, arrowheads).
31. Coreopsis tinctoria
Dyssodia tenuiloba (DC.) B. L. Robinson

"Dyssodia", material grown from commercially available seed in the greenhouse. The original distribution of the species is from Texas to Northern Mexico.

Organogenesis sequence: Disk-Co, S, P, G Ray-Co, P, G

Scale: Bars in Figures 1-3, 7-12, and 14-21 = 50 μm
Bars in Figures 4-6, 13, and 22 = 500 μm

Dyssodia tenuiloba is a low, much branched taprooted annual or short-lived perennial. The heads are numerous and are located terminally on the many branches. Each head has about 30-50 yellow disk flowers, and 5-10 yellow ray flowers on a head. The ray flowers are arranged in a single series.

Inflorescence--The inflorescence meristem is hemispheric before the appearance of any floral primordia (Fig. 1). Floral primordia are initiated rapidly in an acropetal sequence, and the disk flower primordia expand to the plug stage (D in Fig. 2), also in acropetal sequence (D in Fig. 2). Organogenesis on the head begins with those disk flower primordia located peripherally (Fig. 3, unlabelled arrowheads), proceeding acropetally. The ray flower primordia lag behind the disk flower primordia in developmental stage (Figs. 3 and 4,
32. Dyssodia tenuiloba
arrowheads labelled R). As development progresses, the ray flowers gradually begin to catch up to the disk flowers in size (Fig. 5). During late stages of expansion and elongation, the recaptacle broadens and flattens somewhat (Fig. 6).

**Disk flower**--The primordia of the disk flowers rapidly enlarges to the plug stage (P in Fig. 7), and then develops a corolla ring meristem apically (Fig. 7, primordium with arrowhead labelled M), as the first sign of organogenesis. The individual corolla lobes arise from the corolla ring meristem in rapid sequence (Fig. 8, arrowheads). After enlargement of the corolla lobes, the five stamen primordia are initiated, simultaneously and alternate with the corolla lobes on the slopes of the concave floral apex (Fig. 9, arrowheads). After the appearance of the stamen primordia, the first sign of pappus initiation becomes evident as bulges on the flanks of the flower, located opposite the corolla lobes (Fig. 10, arrowheads). The bulges form the individual plumose pappus members, and additional primordia differentiate during later development to produce a solid ring of plumose bristles (Fig. 13, arrowhead labelled P). The two carpels are initiated on the radial plane (Fig. 11, arrowheads labelled G), appearing after the initial pappus member primordia have enlarged somewhat (Fig. 11, arrowheads labelled P), and the corolla lobes have completely obscured the interior of the flower (Fig. 12, arrowhead at same age flower as in Fig. 11).

**Ray flower**--After initiation, the somewhat angular ray flower primordia enlarge and pass through the plug stage (Fig. 14, arrowheads). A corolla ring meristem is formed (Fig. 15, arrowheads) next. The abaxial and the two lateral portions of the corolla expand, but are not well-defined lobes at this stage (Fig. 16, arrowheads). The adaxial portion of the corolla is
33. Dyssodia tenuiloba
34. Dyssodia tenuiloba
suppressed at this stage (Fig. 17, arrowhead labelled Ad), and does not elongate. At about the same time, the four initial pappus members are appear (Fig. 18, arrowheads labelled P), and the two carpel primordia are initiated (Fig. 19, polar view of flower the same age as in Fig. 18, arrowheads labelled G). As the corolla of the ray flower begins to elongate (Fig. 20, arrowheads), the apices of the carpels become appressed and begin to elongate as well (Fig. 21, polar view, arrowheads labelled G). Shortly before anthesis, the corolla has broadened, become inrolled, and the styal branches are evident in a dissected ray flower (C in Fig. 22, arrowheads labelled St).
**Eclipta alba** (L.) Hassk.

"Eclipta", collected from a disturbed site on the Mississippi River levee in East Baton Rouge Parish, Louisiana.

Organogenesis sequence: Disk-Co, S, G, P   Ray-Co, G, P

Scale: Bars in Figures 1-4, 7-13, and 15-21 = 50 μm

Bars in Figures 5, 6, 14, and 22 = 500 μm

The inset of Figure 20 is of the same magnification, different angle.

**Eclipta** is a weakly spreading weed that often roots at the nodes. The heads are located on axillary and terminal peduncles, and only about ten are flowering at any one time, although new heads are constantly formed during the season. There are from 25-35 tetramericous disk flowers per head, 20-30 ray flowers that are of the filiform type.

**Inflorescence**--The meristem of the inflorescence is almost spherical prior to floral initiation (Fig. 1). Floral initiation takes place in a rapid bidirectional sequence (Fig. 2). The larger disk flower primordia are first initiated about halfway up the inflorescence meristem (Fig. 2, arrowheads labelled D). The first ray flower primordia are located proximal to the disk
35. Eclipta alba
flower primordia series (Fig. 2, arrowheads labelled R). Disk flowers are initiated acropetally, and ray flower primordia are initiated in basipetal sequence down to the level of the involucral bracts (I in Fig. 2). The course of development on the head follows the same bidirectional pattern Figs. 3 and 4). The lowermost disk flower primordia are the first to initiate organogenesis (Fig. 3) which then proceeds acropetally for the remaining disk flower primordia (Fig. 4). The ray flower primordia develop in a rapid basipetal sequence on the head, with the largest and most advanced ray primordia located uppermost (Figs. 3 and 4, arrowheads). By the time organogenesis is completed for all the flowers on a head (Fig. 5), equalization has taken place, obscuring any evidence of the early bidirectionality. Numerous corolla trichomes become evident interspersed with the receptacular bracts, (Fig. 6, arrowheads), as the flowers expand during later stages.

Disk flower--The disk flowers are initiated as common primordia acropetally (Fig. 7, arrowhead labelled 1) that subsequently bifurcate in an unequal division (Fig. 7, arrowhead labelled 2). The smaller portion cut off abaxially becomes the receptacular bract primordium, and the adaxial portion is the disk flower primordium. The disk flower primordium enlarges to the plug stage (Fig. 8, arrowhead labelled P), and soon develops a corolla ring meristem apically (Fig, 8, arrowhead labelled M). The receptacular bract primordium also enlarges, in somewhat crowded conditions (Figs. 8 and 9, arrowheads labelled B). The apex of the disk flower primordium becomes concave as the corolla ring meristem enlarges (Fig. 9). Four individual corolla lobes appear as bulges on the corolla ring meristem (Fig. 10, arrowheads labelled C) and the satmens are initiated soon after (Fig. 10, arrowheads labelled S). The corolla lobes arch inward to cover the interior of the disk flower while the
36. Eclipta alba
stamen primordia enlarge (C and S in Fig. 11, partially dissected flower). Slightly later as the corolla develops trichomes (Fig. 12, arrowheads), the two carpel primordia are initiated (Fig. 13, partially dissected flower, arrowheads labelled G). Not until very late in development (Fig. 14) is the pappus initiated as a crown-like enation from the top of the ovary (Fig. 14, arrowheads labelled P). The receptacular bracts have also developed trichomes by this stage (Fig. 14, arrowheads labelled T).

Ray flower--Ray flower primordia are initiated in a basipetal sequence, from a common primordium that also produces a receptacular bract primordium (Fig. 15, arrowheads). The common primordium bifurcates (Fig. 16) to produce the ray flower primordium above and the receptacular bract below (Fig. 16, arrowheads labelled R and B). The ray flower primordia are noticeably smaller than the disk flower primordia from inception onward (Figs. 2-4). The ray flower primordia enlarge to the plug stage (Fig. 17, arrowheads). The corolla ring meristem is the first evidence of organogenesis in the ray flower primordia (M in Fig. 18), initiated well after the neighboring disk flower primordia have begun form differentiation (D in Fig. 18). The corolla ring meristem enlarges evenly initially (Fig. 19, arrowheads labelled 1), until the abaxial portion begins enlargement (Fig. 19, arrowhead labelled 2). The adaxial section of the corolla is suppressed (Fig. 20 and inset, arrowheads labelled D) as the two carpel primordia are initiated (Fig. 20, arrowheads labelled G). As the corolla elongates to form the blade of the ray flower, there is no evidence of individual lobes or teeth (Figs. 21 and 22). Very late in development, the pappus is formed (Fig. 22, arrowheads labelled P). The style has elongated and the stylar branches are evident (Fig. 22, arrowheads labelled St).
37. *Eclipta alba*
Gaillardia aestivalis (Walter) H. Rock.

"Blanket flower", growing in a sandy area in open woods in Allen Parish, Louisiana.

Organogenesis sequence: Disk-Co, P, S, G Ray-Co, P, (S)

Scale: Bars in Figures 1, 2, and 7-21 = 50 μm Bars in Figures 3-6 = 500 μm

Blanket flower is a much branched annual, usually with a tap root. The numerous heads are borne singly on the tips of branches. Each head 60-80 yellow disk flowers and about 10 ray flowers in the material examined.

Inflorescence--The inflorescence meristem is a low dome (Fig. 1) prior to the initiation of the floral primordia. The disk and ray flower primordia are initiated at about the same time on the inflorescence meristem (Fig. 2, arrowheads labelled D and R). The two may be distinguished by their shapes--the disk flower primordia are round, and the ray flower primordia have a half-circular shape. As the primordia enlarge, more disk flower primordia are initiated acropetally in parastichies (Fig. 3). The distinction between the two primordia is lessened compared to earlier stages, although the ray flower primordia are somewhat smaller (Fig. 3, arrowheads labelled D
38. Gaillardia aestivalis
and R). Organogenesis begins with the outermost flowers and proceeds centripetally (Fig. 4). By mid-development, trichomes are differentiating in the outermost disk flowers (Fig. 5, arrowheads). Eventually, all of the flowers become covered with the villous trichomes (Fig. 6).

**Disk flower**—The disk flower primordia rapidly pass through the plug and ring meristem stages (P and M in Fig. 7). The five corolla lobes differentiate in an irregular sequence (Fig. 7, primordia with arrowheads). The corolla lobes are quickly equalized so that all the same size (Fig. 8). After the corolla lobes have arched inward, five bulges located alternate with the corolla lobes on the flanks of the disk flower primordium differentiate next (Fig. 9, arrowheads). The bulges become the setose pappus bristles. Five stamen primordia are initiated next (S in Fig. 10), alternate with the corolla lobes. Two carpel primordia are initiated, and the locule between them forms (Fig. 11, arrowheads labelled G and L). The apices of the carpels elongate and become appressed (G in Fig. 12) so that the locule is internalized. The five pappus members elongate and numerous trichomes differentiate in later stages of development (Fig. 13).

**Ray flower**—After passing through the plug stage (Fig. 3) the ray flower primordia display an irregular corolla ring meristem (Fig. 14, arrowheads) that rapidly differentiates into an abaxial lobe and two lateral lobes (Fig. 15, arrowhead). As the lobes enlarge, the pappus is initiated (Figs. 17 and 18, arrowheads labelled P). The ray flowers of this species are neuter, and other than a brief suggestion of what may be stamens barely initiated in Figure 19 (arrowheads labelled S), there are no other signs of stamens or carpels in the developing ray flower (Figs. 16 and 20). The three corolla
39. *Gaillardia aestivalis*
40. Gaillardia aestivalis
lobes elongate (C in Fig. 21) to produce a strongly three-toothed ligule at maturity (not shown).
Galinsoga parviflora Cav.

"Galinsoga", growing in semi-shade in a low, wet area at the edge of woods in Rockbridge County, Virginia.

Organogenesis sequence: Disk-Co, S, G/P Ray-Co, S, G, P

Scale: Bars in Figures 1-5, 7-11, and 13-17 = 50 μm
Bars in Figures 6, 12, and 18 = 500 μm

Galinsoga parviflora is a low, moderately branched annual herb. The small heads are located terminally on the branches and 15-30 are undergoing anthesis at a particular time. There are about 25 disk flowers and 5-8 disk flowers on a head.

Inflorescence--The inflorescence meristem is rather hemispherical as floral initiation begins (Fig. 1). The receptacular bract primordia seem to intergrade with involucral bract primordia (I and B in Fig. 2). Both the disk and ray flower primordia are initiated in the axils of the two bract types (D and R in Fig. 2). The ray flower primordia appear to lag behind the disks in development and size from the earliest stages (Figs. 2-5). Organogenesis starts with the lowermost disk flowers (D in Fig. 3) and proceeds acropetally. The ray flower primordia undergo organogenesis slightly later (R in Fig. 4). The domed shape of the inflorescence receptacle is
41. Galinsoga parviflora
maintained during later stages of flower differentiation (Figs. 5 and 6).

**Disk flower**—Disk flower primordia arise in the axils of the receptacular bract primordia (Fig. 2 and polar view in Fig. 7, arrowheads labelled D and B). The disk flower primordia enlarge to the plug stage (P in Figs. 8 and 9) and then display a shallow corolla ring primordium (M in Figs. 8 and 9). Four or five individual corolla lobes differentiate from the corolla ring meristem (C in Fig. 9) shortly before the initiation of the stamen primordia. The stamens appear on the inside of the concave floral apex and are alternate with the corolla lobes (S in Fig. 9). Occasionally, a stamen is missing from a series (Fig. 9, arrowhead) in an otherwise pentameric flower. The initiation of the pappus and the carpels happens more or less simultaneously. Individual pappus members are initiated in sequence, beginning with five sites alternate to the corolla lobes (Fig. 10, arrowheads). At the same time, (Fig. 11, polar view of dissected flower of the same age), two carpels have initiated on a radial plane of the head (G). At anthesis, the chaffy pappus (Fig. 12, arrowhead labelled P) surrounds the short corolla tube.

**Ray flower**—The ray flower primordia are rather irregular in shape at initiation (Fig. 13, arrowhead) and are located in the axils of involucral bracts (Fig. 2, bract removed, scar labelled I). After enlargement to the plug stage (R in Fig. 3), a corolla ring meristem is formed apically (M in Fig. 3). Four stamens are initiated (Fig. 14, arrowheads labelled S) in the developing ray flower primordium concomitant with the expansion of three lobes of the corolla. Two carpels are initiated shortly thereafter (G in Fig. 15, the corolla and one stamen have been removed). The corolla and the carpels elongate (Fig. 16) as the
42. Galinsoga parviflora
43. Galinsoga parviflora
pappus primordia are initiated in rapid sequence (arrowheads labelled P). At a slightly later stage, (Fig. 17), the stamen primordia are almost completely resorbed. At anthesis, the three corolla lobes are evident as the apical teeth of the limb of the ray flower.
**Hymenopappus artemisiaefolius** DC.

"Hymenopappus", collected at roadside, at the edge of piney woods in Vernon Parish, Louisiana.

Organogenesis sequence: Co, S, G, P

Scale: Bars in Figures 1-4, and 7-10, = 50 μm

Bars in Figures 5, 6, 11 and 12 = 500 μm

**Hymenopappus** is a biennial taprooted herb that is moderately branched. The heads are discoid and are terminally grouped on the branches in small cymose clusters. There are 12-20 flowers on a head.

**Inflorescence**--The inflorescence meristem is a low dome before any flowers are initiated (Fig. 1). Flower primordia are initiated acropetally (F in Fig. 2). Organogenesis begins with the outermost flowers (Fig. 3; several flowers removed) and progresses inward on the head (Fig. 4, polar view). As the outermost flowers develop trichomes on the corolla surface (Fig. 5, arrowheads labelled T) before the flowers located at the summit of the inflorescence have completed organogenesis (Fig. 5, arrowhead labelled O). By mid-developmental stages (Fig. 6) all the flowers have become equalized in size and stage.
44. *Hymenopappus artemisiaefolius*
Flower--The disk flower primordia are initiated as low mounds (F in Fig. 2), that rapidly enlarge to the plug stage (Fig. 2, arrowheads labelled P). The corolla lobes are simultaneously initiated directly from the apex of the floral primordium (Fig. 3, unlabelled arrowheads). A preceding ring meristem stage occurs only rarely, and is rather irregular when it is expressed (Fig. 4, arrowhead). The corolla lobes rapidly expand and cover the interior of the flower (Fig. 4). The stamen primordia are initiated next (flowers in Fig. 4), simultaneously and alternate with the corolla lobes (S in Figs 7 and 8). Two carpel primordia are initiated (Fig. 9, arrowheads labelled G) after some expansion of the stamens. At this time, the first evidence of the pappus is noticable (Fig. 10, arrowhead labelled P) as a swelling of the upper edges of the developing achene. These swellings expand into a pappus of chaffy scales at maturity (Fig. 11, arrowhead labelled P). At anthesis, (Fig. 12) the tips of the externally trichome bearing stamens (arrowhead labelled S) and the stigma (arrowhead labelled St) are exserted from the corolla.
45. Hymenopappus artemisiaefolius
Madia elegans D. Don.

"Tarweed", obtained from the collection at the University of California Botanical Gardens, at Berkeley. The native range is throughout montane California.

Organogenesis sequence: Disks-Co, S, G Ray-Co, S, G

Scale: Bars in Figures 1-3, 7-13, and 15-21 = 50 μm
Bars in Figures 4-6, 14, 22 = 500 μm

Common Madia, as it is otherwise known, is a handsome moderately branched plant with a copious vestiture of glandular hairs. This annual species attains a height of about 2.5 meters. Heads are terminal on the branches. Each head has about 90 disk flowers and 15 ray flowers; both floral types are yellow.

Inflorescence—The inflorescence meristem is moderately domed at the stage of floral initiation (Fig. 1), bract primordia are also present (B) and may be distinguished by their upcurved apices. Below and between the bract primordia, uncommitted meristematic areas are present (Fig. 1, unlabelled arrowheads). The first disk flower primordia initiate at or above the level of the bract primordia (Fig. 1, arrowheads labelled D). Subsequent disk flower primordia continue to
46. Madia elegans
initiate acropetally (D in Fig. 2), and the ray flower primordia are initiated (Fig. 2, arrowheads labelled R) in the basal meristematic areas below the enlarging bract primordia (B in Fig. 2). Additional bract primordia are also initiated, subtending the disk flower primordia a series higher than the outermost ones (Fig. 2, arrowheads labelled X). Initiation of additional disk flower primordia proceeds acropetally until the inflorescence meristem is used up (Fig. 3). Although the disk and ray flower primordia start out roughly equal in size (Fig. 2), the disk flower primordia quickly surpass the rays in size (D and R in Fig. 3) and stage of development (Fig. 4). Organogenesis begins with the outermost disk flowers (Fig. 4) and proceeds acropetally. The ray flower primordia are suppressed until several series of disks have differentiated (D and R in Fig. 5). The bracts that subtend the outermost two series of disk flowers enlarge and broaden to cover the disk flower (B in Fig. 5). At mid-development, the copious vestiture can be seen on all structures of the inflorescence except the developing ray flowers (Fig. 6, arrowheads labelled R). The disk flower bracts have elongated and extend beyond the head (B in Fig. 6).

Disk flower.--The disk flower primordia are rounded protuberances when they initiate (Figs. 1 and 2), and they rapidly expand to the plug stage (P in Fig. 7). A corolla ring meristem is seen only briefly (M in Figs. 7 and 8) before the five corolla lobes become evident (C in Fig. 8). Five stamen primordia are initiated next alternate with the corolla lobes and simultaneously (S in Figs. 8 and 9). The corolla lobes begin to expand (C in Fig. 10) and arch over the interior of the flower (Fig. 5). After the stamen primordia have enlarged somewhat (S in Fig. 11), the two carpel primordia are initiated, of which the first evidence is the appearance of a groove (Fig. 12, arrowhead labelled Gr). The two carpels arise on either side of
47. Madia elegans
the groove, and become apressed (G in Fig. 13). At anthesis, the anthers dehisce longitudinally (Fig. 14, arrowhead labelled A) releasing their pollen.

**Ray flower**—Ray flower primordia are initiated in the bare meristematic areas at the base of the inflorescence meristem (Fig. 15, arrowheads). The primordia enlarge to the plug stage (Fig. 2 arrowhead labelled R). Organogenesis begins with the enlargement of the two lateral corolla lobes (Fig. 16, arrowheads). As the abaxial corolla lobe begins to enlarge (Fig. 17, arrowheads labelled Ab), four stamen primordia are initiated (Fig. 17, arrowheads labelled S). Two carpel primordia are initiated (G in Fig. 18) as the three corolla lobes enlarge. The corolla of the ray flower starts to elongate by zonal growth below the three lobes (Fig. 19); at the same time, the stamen primordia are in the process of resorption (Fig. 20, arrowhead labelled S). At later stages of development, the stamens are no longer obvious (Fig. 21). At anthesis, the corolla unfurls and the style is exserted (Fig. 22, arrowhead labelled St).
48. Madia elegans
Rudbeckia laciniata L.

"Coneflower" or "Golden glow", collected from a low, moist area in dense woods in West Feliciana Parish, Louisiana.

Organogenesis sequence: Disks-Co, S, G, Ray-Co

Scale: Bars in Figures 1, 2, 7-14, and 16-21 = 50 \( \mu m \)

Bars in Figures 3-6, 15, 22 = 500 \( \mu m \)

Rudbeckia laciniata is a tall perennial herb that branches moderately. Heads are located terminally on the branches. There are approximately 150 yellowish disk flowers and 10 to 15 yellow rays on each head.

Inflorescence--The inflorescence is a low dome before the advent of floral initiation (Fig. 1). Receptacular primordia are initiated at the base of the inflorescence (Fig. 2, arrowheads labelled B) and proceed acropetally. Almost immediately, disk flower primordia are initiated in the axils of the receptacular bract primordia (Fig. 2, arrowheads labelled D). At the base of each bract/disk parastichy a small uncommitted meristematic area remains (Figs. 2 and 3, arrowheads labelled R), from which the ray flower primordia are formed (Fig. 4, arrowhead labelled R). As initiation of the disk flowers and receptacular bracts proceed acropetally on the head, the inflorescence
49. Rudbeckia laciniata
receptacle gradually elongates (Figs. 1-6) and becomes cone-shaped in later stages. The receptacular bracts quickly elongate and cover the disk flower primordia (Figs. 4 and 5, arrowheads labelled B; many bracts have been dissected away). Organogenesis on the head begins with the lowermost disk flowers (Fig. 5, arrowheads labelled D), and proceeds acropetally (Fig. 6, arrowheads labelled D). The ray flowers display minimal development at this stage (Fig. 6, arrowheads labelled R).

**Disk flower**--The disk flower primordia are initiated (Fig. 7, arrowheads labelled D) in the axils of subtending receptacular bract primordia (B in Fig. 7). The primordia enlarge to the plug stage (Fig. 8), and then develop a corolla ring meristem apically (Fig. 9, arrowheads). Five corolla lobes are formed next from the corolla ring meristem (C in Fig. 10), more or less simultaneously. As the corolla lobes enlarge and begin to arch inward (Fig. 11, arrowheads labelled C), the five stamen primordia are initiated simultaneously (Figs. 11 and 12, arrowheads labelled S), in alternation with the corolla lobes. After the corolla lobes have obscured the interior of the disk flower (Fig. 13), the two carpel primordia initiate (Fig. 14, arrowheads labelled G) on a radial plane. Later in development, the corolla tube has elongated, and the hairy tips of the style branches have differentiated (Fig. 15, arrowheads labelled C, ST). A pappus was not seen in the material collected.

**Ray flower**--The ray flower primordia are initiated (Fig. 16, arrowhead labelled R) from the small irregular areas of uncommitted meristem at the base of each disk parastichy. The primordium slowly expands (Fig. 17). The presence of two bulges laterally is the first sign of organogenesis (Fig. 18, arrowheads). As the two lateral corolla lobes expand by zonal
50. **Rudbeckia laciniata**
51. *Rudbeckia laciniata*
growth, they become more or less united by the outgrowth of the abaxial portion of the corolla (Figs. 19 and 20, arrowheads labelled Ab). If the corolla is dissected away at this stage, it is evident that no additional organs are initiated (Fig. 21). Later in development, the ray corolla has expanded, become folded over, and two apical teeth are visible (Fig. 22, arrowheads).
Tithonia rotundifolia Blake.

"Mexican sunflower", grown from commercially available seed in the greenhouse. This species is native to Mexico, hence its common name.

Organogenesis sequence: Disks-Co, S, G/P Ray-Co, S, G, P

Scale: Bars in Figures 1, 2, 6-10, and 13-17 = 50 μm
Bars in Figures 3-5, 11, 12, 18, and 19 = 500 μm

Mexican sunflower is a tall (3-4 meters) robust annual that is moderately branched. The numerous heads are terminal on the branches, borne on hollow peduncles, and are quite attractive with yellow disk flowers and deep orange rays. Each head has 75-90 disk flowers and 16 ray flowers.

**Inflorescence**—Prior to floral initiation, the inflorescence meristem is low-domed and almost flat (Fig. 1). Each disk flower primordium and receptacular bract primordium are initiated from a common primordium; the first ones are located on the periphery of the inflorescence (Fig. 2, unlabelled arrowheads). The common primordia rapidly bifurcate, roughly into two equal halves, and the upper portion becomes the disk flower primordium and the lower, the receptacular bract primordium (Fig. 2). The ray flowers are initiated as
52. Tithonia rotundifolia
independent primordia (Fig. 2, arrowheads labelled R), after two or three series of disk flower primordia are present. The ray flower primordia are triangular in shape and are located at the base of each disk flower parastichy (Fig. 2). Initiation of additional common primordia proceeds centripetally (Fig. 3, polar view) and as the last common primordia are initiated at the summit of the inflorescence meristem (Fig. 3, unlabelled arrowhead). The peripherally located disk flower primordia begin organogenesis (Fig. 3, arrowheads labelled O). The course of organogenesis on the head proceeds acropetally (Figs. 3 and 4), but is obscured by the rapidly elongating receptacular bracts (B in Fig. 4). The ray flower primordia (Figs. 3 and 4, arrowheads labelled R) are suppressed, so that the disk flowers have surpassed the rays in developmental stage. The bracts elongate and become coriaceous (B in Fig. 5) protecting the head in bud. In addition, the ray flower corollas have caught up to the disk flowers in size (R and D in Fig. 5)

**Disk flower**—Common primordia are initiated on the surface of the inflorescence meristem (CP in Fig. 6); they rapidly bifurcate (Fig. 6, arrowhead labelled X). The bifurcation is about equal, and the abaxial portion becomes the receptacular bract primordium, and the adaxial portion becomes the disk flower primordium (B and D in Fig. 6). As the disk flower primordia enlarge, they rapidly pass through the plug stage (P in Fig. 7), and the corolla ring meristem stage (M in Fig. 7). Five corolla lobes differentiate simultaneously (C in Fig. C) from the corolla ring meristem. Five stamen primordia appear next, simultaneously and alternate with the corolla lobes (Fig. 8, arrowheads labelled S). After the corolla lobes have expanded, the two carpel primordia are initiated (Fig. 9, arrowheads labelled G) on a radial plane of the head. Concommitently, two bulges appear on the summit of the achene (Figs. 9 and 10, arrowheads labelled P; adaxial bulge
53. Tithonia rotundifolia
not in field of view), located abaxially and adaxially, that will become the awns and/or scales that comprise the pappus. The style begins to elongate (St in Fig. 10) by zonal growth. During later stages (Fig. 11, arrowheads labelled SB; some stamens removed) the stylar branches develop numerous papillary trichomes on the outer surfaces). A disk-like nectary (arrowhead labelled N) forms around the base of the style (St). At maturity, the base of the corolla tube enlarges to form a nectar receptacle (NR in Fig. 12), and the mature form of the pappus can be seen as scales (Fig. 12, arrowheads labelled P) at the top of the achene.

Ray flower--The ray flower primordia are triangular in shape when they appear (Fig. 13, arrowheads labelled R). The primordia enlarge (Fig. 14) and then the lower edge begins to expand as an elongated arcuate mound (Fig. 15, arrowhead) to form the ray corolla. By this stage, the ray flower primordium has become bilaterally flattened and will remain so (Figs. 15-18) throughout development. The corolla expands equally, without the appearance of individual lobes, and two stamen primordia are initiated in lateral positions (S in Fig. 16). As the corolla elongates (C in Fig. 17) two carpel primordia are initiated (Fig. 17, arrowheads labelled G) in a radial plane. Later, the stamen and carpel primordia are resorbed (Fig. 18), leaving no trace. As the corolla elongates (Fig. 19), its edges fold over and the achene shows some evidence of a rudimentary pappus (Fig. 19, arrowheads labelled P).
54. Tithonia rotundifolia
Tribe: Inuleae

In the tribal treatment by Merxmuller et al. (1977), the Inuleae includes two "enlarged" subtribes, the Inulinae *sensu amplo* and the Gnaphaliinae *sensu amplo*, and a third tribe, the Arthrixiinae *sensu amplo*, that is intermediate between the first two. This grouping was based on pollen, style, and karyological data. Bremer (1987) disagreed, treating the Inuleae as a paraphyletic grouping, and breaking the tribe down to three operational taxonomic units (OTU). Each OTU was apparently given tribal status in Bremer's preliminary phylogenetic study of the entire family. I selected *Gnaphalium purpureum* to represent the Gnaphaliinae *sensu amplo* of Merxmuller et. al (1977), or Bremer's (1987) Gnaphalieae. *Pluchea foetida* is selected to represent the Inulinae *sensu amplo* of Merxmuller et al., or Bremer's (1987) Inuleae-Plucheinae *sensu lato*. 
Gnaphalium purpureum L.

"Cudweed", collected on the Louisiana State University campus in Baton Rouge, Louisiana.

Organogenesis sequence: Disks-Co, S/P, G Filiform-Co, P, G

Scale: Bars in Figures 1-6, 8-19 = 50 μm
Bar in Figure 7 = 500 μm

Gnaphalium purpureum possesses numerous heads on very short branches from one main inflorescence axis that emerges from a basal rosette of leaves. The bisexual (disk) flowers number from 3-5, and with about 90 peripheral or filiform flowers.

Inflorescence--Prior to initiation of flowers, the inflorescence apex of Gnaphalium purpureum is turbinate with a conical tip (Fig. 1, inflorescence at lower right). The peripheral or filiform flower primordia are the first to be initiated. Seven to eight flowers per parastichy form, starting at the constricted base of the inflorescence then proceeding acropetally (Fig. 2). The terminal inflorescence in Figure 1 shows all of the filiform flower primordia initiated, with just the beginnings of one of the first disk flower primordia (arrowhead). Three to five disk flower primordia are initiated
55. Graphium purpureum
lastly around the summit of the inflorescence (Fig. 3), and are noticeably larger at comparable stages than the filiform flower primordia. Organogenesis of the filiform flowers on the head is synchronous (Figs. 4-7), with all filiform flowers at almost exactly the same stage and size at all times. The disk flowers are not as tightly synchronized among themselves (Figs. 4, 5), but it is a moot point to try to assess acropetal directionality of ontogenetic stages among only three to five flowers. At stages close to anthesis (Fig. 7), the abundant pappus, which serves in wind dispersal of the achene, is highly evident.

**Disk flower**--The bisexual or disk flowers are produced last on the flanks of the inflorescence apex, are rather widely spaced, and do not appear to fit along any parastichies of the filiform flower primordia (Fig. 8). A corolla ring meristem appears (RM in Fig. 8), which then differentiates into five corolla lobe primordia (C in Fig. 9, polar view of inflorescence). The flower broadens and flattens (Fig. 10, arrowhead) before the stamens and pappus ring primordium initiate roughly simultaneously (S, P in Fig. 11). The individual pappus members (Fig. 12, arrowheads labelled P, polar view of inflorescence) differentiate from the ring meristem at about the same time as the initiation of the two carpel primordia (Fig. 12, arrowheads labelled G). The numerous pappus members per flower rapidly elongate during mid-development, while the stamens and style undergo differentiation (Fig. 13).

**Filiform flower**--Initiation of the filiform flower primordia begins at the constricted base of the inflorescence, below the widest diameter of the inflorescence meristem (F in Fig. 14). The primordia are sequentially initiated in orderly parastichies (Fig. 15, polar view of inflorescence), converging
56. Gnaphalium purpureum
57. Gnaphalium purpureum
on the inflorescence apex. Once all the flowers are initiated, however, they become synchronized such that all the filiform flowers on an inflorescence display the same stage of development at any one time (Figs. 16-19). After their initiation, the primordia enlarge into the plug stage (Fig. 16). The corolla ring meristem becomes evident next (Fig. 17, arrowheads labelled RM). Just below the developing corolla, the pappus ring meristem is the next to appear (Fig. 18, arrowheads labelled P). The numerous individual pappus members differentiate from the pappus ring meristem shortly thereafter (Fig. 19, arrowheads), before the formation of the two carpel primordia are initiated last (not shown). No stamens are initiated. At maturity, the corolla tube of the filiform flowers is long and unexpanded (Fig. 7) and achenes of both flower types display numerous surface papillae (Fig. 7).
**Pluchea foetida** (L.) DC.

"Marsh-fleabane" collected from a wet roadside ditch in Jefferson Davis Parish, Louisiana.

Organogenesis sequence: Disks-Co, P, S, G Filiform-Co, P, G

Scale: Bars in Figures 1-4, 7-11 and 13-18 = 50 μm
Bars in Figures 6, 12 and 19 = 500 μm

This herbaceous species has many (20-40) inflorescences per plant, roughly arranged in a flat-topped synflorescence. There are usually about 3-5 bisexual flowers and 140 filiform flowers. Occasional malformed heads were also noted, seemingly a result of an early fusion between two inflorescence meristems (not shown).

Inflorescence--The inflorescence meristem of *Pluchea foetida* is high-domed and rather turbinate (Figs. 1-4), and the receptacle retains this shape through anthesis (Fig. 6), although by then the flat surface is proportionally much larger. The filiform flowers are the first to initiate and seem to appear first at the distal ends of their parastichies rather than at the base (Figs. 1-3, arrowheads labelled F). In other words, they are initiated basipetally on the capitulum. After the appearance of the first filiform primordia, successive
58. Pluchea foetida
primordia are initiated basipetally on the inflorescence, to fill the bare meristematic areas at the base of the inflorescence (Figs. 2, 3, arrowheads labelled B). Concurrently, three to five bisexual disk flowers are initiated high on the flanks apex of the inflorescence meristem (D in Fig. 3). Thus floral initiation is bidirectional See Fig. 1, p. 52) because the disk flowers are initiated acropetally. The disk flowers, although the last to be initiated, are the first to undergo organogenesis (Fig. 4). Order of floral organogenesis is sequential on the capitulum. The most distal filiform flowers are the first to undergo organogenesis (Fig. 5, arrowheads), and subsequent organogenesis of the filiform flowers on the head proceeds basipetally, following the order of initiation (Fig. 5).

**Disk flower**—After expansion to the plug stage (Fig. 7, primordium labelled P), disk flower primordia develop apical corolla ring meristems (RM in Fig. 7). Five corolla lobe primordia are formed from the ring meristem shortly thereafter (Fig. 8, arrowheads), followed by the appearance of the pappus (Fig. 9, arrowheads). The stamens (S in Fig. 10, dissected flower with corolla removed) are initiated after the pappus members and the corolla tube (CT) have elongated and the corolla lobes have become appressed. Two carpel primordia are later initiated (G in Fig. 11). The stamens (S) have not enlarged appreciably at this time, but the pappus members (P) have elongated and begun to differentiate. At anthesis, the stamens and style are just barely exserted from the corolla lobes (Fig. 12, stamens labelled S, style labelled G).

**Filiform flower**—After all filiform floral primordia are initiated in basipetal order, each expands into the plug stage (Fig. 14). Order of organogenesis is sequential and basipetal on the head. The uppermost flower primordia begin organogenesis
59. *Pluchea foetida*
60. *Pluchea foetida*
with the formation of a corolla ring meristem (RM in Fig. 15). Subsequently, the pappus is formed, first as a ring meristem subtending the corolla (Fig. 16, arrowheads labelled RM), which then gives rise to individual pappus members (Fig. 16, at top). As the corolla tube enlarges, three corolla lobes are delineated somewhat randomly (Fig. 16, arrowheads labelled C, at top). The basipetal course of development can clearly be seen in Figure 17. Two carpel primordia are initiated after the corolla has elongated to obscure the interior of the flower. In Figure 18 two corolla lobes (C) and one carpel (G) are visible; one corolla lobe and one carpel primordium have been removed. There is no sign of any staminodial structure at any point in development. In Figure 19, the upper quarter of both flower types is seen at anthesis, the delicate filiform flower on the left and the large disk flower at right.
Tribe: Senecioneae

Two subtribes are currently recognized (Nordenstam, 1977); the Senecionineae with 96 genera (including Senecio, the most speciose genus in the plant kingdom) and the Blennospermatineae with four small genera. Within the Senecionineae, there are two main "complexes", the "cacalioid", represented here by Cacalia plantaginea, and the "senecioid". Senecio glabellus represents a radiate example of the "senecioid" complex, and Gynura sarmentosa a discoid. No members of the Blennospermatineae were available.
Cacalia plantaginea (Raf.) Shinners.

"Indian plantain" collected along fenceline of pasture at roadside in Tangipahoa Parish, Louisiana.

Organogenesis sequence: Co, S, P, G

Scale: Bars in Figures 1-8 = 50 μm

Bars in Figures 9-12 = 500 μm

This stout herbaceous species usually produces about 20-30 heads per plant, located terminally on the upper branches of the main inflorescence axis. Each head contains from 4-6 flowers.

At the onset of flowering, the inflorescence apex of this species appears very like a vegetative apex; it is rather orthogonal rather than round in outline with a roughly 2/5 phyllotaxy of involucral bracts (Fig. 1). The bracts may be distinguished from the flower primordia by their broad insertion (Fig. 2) and their upcurved nature which is apparent almost immediately after their initiation. The four to six flowers are initiated roughly centripetally (Fig. 2). There are no peripheral or ray flowers present in Cacalia plantaginea; all flowers are disciform.
61. Cacalia plantaginea
Figure 2 shows four recently initiated flower primordia, with the two older primordia located relatively farther away from the inflorescence apex (at arrowhead). The two inner flower primordia have initiated after the outer primordia and their size variation reflects their successive initiation. This size and stage differential persists until anthesis. Organogenesis proceeds in a roughly centripetal fashion in each head; however, due to the expansion of the receptacle and the relatively small number of flowers present on each inflorescence head, the centripetal pattern is all but obscured.

The flower primordia expand into rounded peg shapes (Fig. 3) whose apices then flatten (Fig. 3, at right). Four or five corolla lobe primordia are the first recognizable organs (C in Fig. 4) and they appear simultaneously at the "corners" of each of the floral apices. Flowers on an individual inflorescence may be all tetramerous, all pentamerous, or a mixture of the two types. Very soon after, stamen primordia initiate alternipetalously (S in Fig. 5) as the corolla lobe primordia begin to enlarge and curve inward. Next to arise is the pappus, which is first evident as a swelling below the corolla lobes (Fig. 6, arrowhead labelled P) and will differentiates into numerous individual primordia simultaneously (Fig. 7). At this stage, the corolla lobes have grown inward and become appressed so that the concave apex of the flower where the two carpels are initiated is obscured. As the corolla tube elongates by zonal growth below the free corolla lobes, the lobes seem to lag behind the more accelerated elongation of the stamens and carpels (Figs. 8, 9, 10). As result, the stamens and carpels protrude from the corolla (S in Figs. 9, 10, arrowheads labelled G) for a period during mid-development. Eventually, the corolla tube and lobes catch up and once again conceal the interior of the flower (Fig. 11) until anthesis (Fig. 12).
62. Cacalia plantaginea
Gynura sarmentosa DC.

"Purple velvet plant", originally from the West Indies, obtained from the greenhouse collection at the Missouri Botanical Garden.

Organogenesis sequence: Co, P, S, G

Scale: Bars in Figures 1-3 and 7-11 = 50 µm
Bars in Figures 4-6 and 8 = 500 µm

The purple velvet plant, a lax trailing succulent herb, displays numerous heads when flowering. The heads are in terminal corymbiform synflorescences with about 30 heads in each synflorescence. About 30-40 disk flowers are present on each head; there are no ray flowers.

Inflorescence--The bare inflorescence apex (Fig. 1) is relatively broad and convex. Involucral bracts initiate in helical order along very shallow parastichies at the edges of the inflorescence apex and immediately begin to elongate. Disk flower primordia (there are no rays in this species) begin to initiate acropetally along spiral parastichies, distal to the most recently initiated involucral bracts on the head (Fig. 2). As more flowers are produced (Fig. 3), the receptacle of the inflorescence broadens and flattens so that by mid-
63. *Gynura sarmentosa*
development the inflorescence has almost lost its initial domed aspect. The inflorescence apex diminishes in diameter as more flowers are initiated. By anthesis, all involucral bracts appear to be inserted on the same level (that is, not imbricate) although originally they are formed sequentially in shallow parastichies on different levels. Organogenesis begins first in the peripheral flower primordia (Figs. 4, 5) and is acropetal on the head, following the order of initiation. After organogenesis (Fig. 6) all flowers appear to have equalized in developmental stage and are synchronous.

**Flower**—After initiation (Fig. 2, 3), flower primordia expand into the typical Asteraceous peg shape (Fig. 7) which flattens and then exhibits an apical depression. Around this depression the five corolla lobe primordia form simultaneously (Fig. 8, arrowhead) and expand, the median lobe is abaxial. Shortly thereafter the corolla tube starts to lengthen (Figs. 9, 10) by zonal growth. Very soon after the expansion of the corolla lobes, the pappus is initiated, girdling the flower midway as an undifferentiated primordial zone (Fig. 8, arrowhead labelled P). The stamens are initiated more or less simultaneously and alternate with the corolla lobes (Figs. 9, 10, arrowheads labelled S) (a slight difference in size of early stages of stamen primordia is noticeable but unequivocal evidence of spiral initiation was not obtained). Concurrently with stamen initiation, particular zones of the pappus ring meristem begin to differentiate into the individual pappus members, generally starting with those regions that are not closely abutted to a neighboring flower. Two carpels are initiated (G in Fig. 11) after the corolla lobes have incurved to conceal the interior of the flower. The two are always arranged medianly (i.e., both lie on the same radius of the inflorescence). Shortly before anthesis (Fig. 12), the pappus members have elongated greatly, as well as the corolla tube and the style.
64. Gynura sarmentosa
**Senecio glabellus** Poiret

"Yellowtop" or "Butterweed", collected from the field in East Baton Rouge Parish, Louisiana.

Organogenesis sequence: Disks-Co, P, S, G  Rays-Co, P, S, G

Scale: Bars in Figures 1-5, 7-11 and 13-17 = 50 μm  
Bars in Figures 6, 12 and 18 = 500 μm

In this herbaceous species, the main inflorescence axis arises from a basal rosette of leaves and is unbranched for the bottom 2/3 of its length. There are several orders of branching, and each branch is terminated by an inflorescence. The grouping of the numerous (50+) inflorescences is roughly corymbiform. On each head, there are about 100 disk flowers, and 12-18 ray flowers arranged in a single series.

Inflorescence--Individual inflorescences arise on the main inflorescence axis (Fig. 1) in the axils of inflorescence bracts. As each inflorescence apex enlarges, it begins to produce involucral bracts along shallow parastichies (Fig. 2). It is late broadening of the receptacle that brings about the uniseriate appearance of the involucral bracts at, or shortly before, anthesis. Disk flowers are the first to begin floral initiation
65. *Senecio glabellus*
(Fig. 2, arrowheads labelled D), arising acropetally in shallow spirals and in helical order, leaving a roughly triangular space uncommitted at the base of each parastichy (Fig. 2, arrowhead labelled R). These spaces are soon filled by formation of ray flower primordia (Fig. 3, arrowheads labelled R), whose development will continue to lag behind that of the disk flowers until mid to late development. The acropetal sequence of organogenesis on the inflorescence is initiated by the outermost disk flowers (Fig. 4) followed shortly thereafter by the ray flowers (Fig. 5, arrowhead labelled R). In figure 6 (arrowhead labelled R), the tetramerous rays are only beginning to catch up in size to the pentamerous disk flowers.

**Disk flower**—The disk flowers, which start out as rounded primordia (Fig. 3), flatten apically and each develops a corolla ring meristem, while the apex of the flower primordium becomes depressed (Fig. 7). Shortly thereafter, five corolla lobes differentiate simultaneously (Fig. 8, flower on left) with the median lobe located more or less adaxially (unlike the prevailing pattern in Asteraceae in which the disk flowers have the median corolla lobe located abaxially). The pappus is next to appear, arising as a ridge encircling the flower (Figs. 8, 9, flowers with arrowheads labelled P) upon which the individual pappus members will appear (Fig. 10). Concurrently, the corolla lobes have begun to arch inward and the tube has started to elongate. Stamen primordia are next to initiate (S in Fig. 9) and do so simultaneously and alternipetalously. As the flower expands (Fig. 10) the individual pappus members begin to differentiate in five zones opposite the stamens. Additional pappus members fill in the gaps from both directions as development progresses (Fig. 11). The two median carpels are the last organs to arise (Fig. 11, arrowheads labelled G) shortly after the differentiation of pappus members. At anthesis (Fig. 12) the perfect, fertile disk
66. *Senecio glabellus*
flower has numerous bristle-like pappus members (some have been removed) and a longitudinally ridged achene.

Ray flower--The heretofore uncommitted triangular zone (Fig. 2, arrowhead labelled R) at the base of each parastichy on the head produces initially triangular ray flower primordia (Fig. 13, arrowheads). These become consistently tetramerous (Fig. 14), although the absolute shape varies somewhat at this stage apparently due to space limitation (Figs. 4, 5, arrowheads labelled R). A corolla ring meristem is first to develop (RM in Fig. 14) and eventually differentiates into four more or less equal corolla lobes (C in Fig. 15). As in the disk flower, the pappus ring meristem, located below and encircling the corolla, next becomes evident (Fig. 16, arrowhead labelled P). Evident only for a brief period during development, four alternipetalous stamen primordia are initiated simultaneously (S in Fig. 16). As the lateral and abaxial corolla lobes expand by intercalary or zonal growth, the stamens are aborted, resorbed, and are no longer evident (Fig. 17). At about the same time, two carpel primordia are initiated (G in Fig. 17), oriented on the median plane of the flower (or radially on the head). The carpel apices elongate and form the paired stigmatic branches seen at anthesis in Figure 18 (St).
67. Senecio glabellus
Tribe: Arctoteae

Four subtribes are proposed for the Arctoteae by Norlindh (1977a). The majority of the species in this tribe are in the two larger subtribes, the Arctotinae and the Gorteriinae. Two subtribes, the Gundeliinae and the Eremothamninae, are monotypic. Robinson and Brettell (1973) give the Eremothamninae tribal status, while Leins (1970) proposes subtribal status in the Arctoteae, the treatment later adopted by Norlindh (1977a). The Gundeliinae are typified by the aggregation of the heads into heads of a second order (Norlindh, 1977a), also termed an "incapitulescence" (Petit, 1988). In an elegant developmental study of the inflorescences, floral groups, flowers, and fruit complexes of Gundelia tournefortii, Classen-Bockhoff et. al. (1989) have demonstrated that the aggregation in G. tournefortii is of a tertiary nature.

As the Arctoteae are primarily African in distribution, living plants were difficult to procure. Luckily, some Arctoteae are of horticultural importance and preserved material was collected from cultivated species. Venidium fastuosom, grown from seed, represents the subtribe Arctotinae, and Gazania rigens the subtribe Gorteriinae. Material was not available from either of the monotypic subtribes, but comparisons and conclusions will be drawn from the more than adequate study by Classen-Bockhoff (1989).
\textit{Gazania rigens} Sims.

"Gousblom" or "Gazania", grown from commercially supplied seed in greenhouse, originally from SW Africa.

Organogenesis sequence: Disks-Co, S, G, P Rays-Co

Scale: Bars in Figures 1-2, 7-12 and 14-20 = 50 \( \mu \text{m} \)

Bars in Figures 3-6 and 13 = 500 \( \mu \text{m} \)

This perennial rosette plant sends up one or two scapes at a time from the leaf axils. Each scape is unbranched, lacks leaves and is terminated by the single showy inflorescence. Head size (number of flowers) is variable, at least in the cultivated specimens. In the plants obtained for the current study, the heads were usually made up of 90-180 central disk flowers and 15-30 ray flowers of brilliant color and arranged in a single series.

\textbf{Inflorescence}--The inflorescence apex is high-domed prior to flower initiation in this species (Fig. 1). The first flowers to initiate are the disk flowers (D in Fig. 2) leaving an uncommitted meristematic region at the base of each parastichy (Fig 2, arrowheads labelled R) where the ray flower primordia will form when approximately half of the total disk flowers have been initiated. In Figure 3, all disk and ray
68. Gazania rigens
flower primordia have been initiated, organogenesis has begun in them, and is proceeding acropetally on the head. The ray flowers are somewhat suppressed in size compared to the disk flowers (Fig. 3, arrowheads). At this stage zonal growth causes the involucral bracts to become basally united to form a cylinder encompassing the developing inflorescence (Z in Figs. 3-6), a characteristic of this subtribe. At the same time, the receptacle loses its domed shape, and becomes almost flat, and expanding before anthesis (Figs. 5, 6).

**Disk flower**--Rounded disk flower primordia (Fig. 7) arise on the lower flanks of the dome-shaped inflorescence apex, and soon expand into cylindrical plug-stage primordia (Fig. 8, arrowhead); rapidly, without an intervening ring meristem stage, five corolla lobes appear (Fig. 8, flowers labelled C). Stamens are initiated soon thereafter (Fig. 9) or almost simultaneously. The upper flower in Figure 9 shows the beginning of stamen initiation, with one stamen present (arrowhead), while the lower flower has completed stamen initiation. The corolla tube (CT in Fig. 10) elongates, and the corolla lobes arch inward to cover the interior of the flower. After some elongation of the stamen primordia (Fig. 11, S), two carpels are initiated, (G in Fig. 11). The pappus is the last organ set to appear (P in Fig. 12), arising as individual members relatively late, as trichomes become differentiated on the surface of the corolla (Fig. 12, arrowheads). At anthesis (Fig. 13) the corolla lobes are loosely held together by trichomes located on the apices of the lobes.

**Ray flower**--The ray flower primordium is initiated in a triangular area on the receptacle and retains its triangular shape (R in Figs. 1, 2) until the corolla arises. The corolla becomes recognizable as two arcuate mounds, with gaps
69. Gazania rigens
70. Gazania rigens
adaxially and abaxially (Fig. 16). Zonal growth of the corolla below the level of the gaps produces a short corolla tube (CT) with a larger slit adaxially than abaxially (CT in Fig. 17, polar view of flower). The dissected ray flower seen in transection in Figure 18 demonstrates the total suppression in further organogenesis--no vestigial organs such as staminodis are initiated, and the flower is sterile at maturity. At mid-development the two slits may still be seen (Fig. 19); and at anthesis (Fig. 20) the abaxial slit is evident between the two apical teeth, while the corolla unfurls from the adaxial slit.
Venidium fastuosum Stapf.

"Monarch of the Veld", grown from commercially supplied seed in greenhouse, originally from SW Africa, the region known as Namaqualand.

Organogenesis sequence: Disks-Co, S, G       Rays-Co, S, G

Scale: Bar in Figure  11 = 5 μm
Bars in Figures 4-8, 10 and 13-18 = 50 μm
Bars in Figures 1-3, 9, 12 and 19 = 500 μm

Venidium fastuosum is a somewhat trailing wooly herb with many inflorescences. Heads are terminal on the numerous side shoots. Each head contains ca. 200 disk flowers and about 40 ray flowers.

Inflorescence--Due to cultivation difficulties, complete developmental sequences were not obtained. The earliest stage obtained may be seen in Figure 1. The rounded disk flower primordia (D) are initiating acropetally towards the apex of the inflorescence meristem which is curiously concave. Ray flower primordia may be distinguished by their slightly more irregular shape (Fig. 1, arrowheads). Unfortunately, it is not possible to ascertain which floral type
71. Venidium fastuosum
was initiated first in Figure 1, but Figure 2 shows that the ray flowers (R) lag behind in development. The inflorescence no longer has a concave apex by the time all the disk flowers are present (Fig. 2); it broadens considerably after all organogenesis is completed (Fig. 3).

**Disk flower**—Disk flower primordia are initiated as rounded protuberances, acropetally along orderly parastichies (Fig. 4, arrows labelled D). An apical corolla ring meristem is not formed in this species. The five corolla lobes (Fig. 5, flower on right labelled C) arise directly from the plug stage (Fig. 5, flower to the left with arrowhead). The stamens are the next set of organs to appear (Fig. 6, arrowheads) after the corolla lobes have expanded somewhat. Stamens appear to be initiated simultaneously. When the length of the corolla tube (CT in Fig. 7) is about equal to the length of the individual corolla lobes, the two carpels are initiated (G in Fig. 8). (Figure 7 and Figure 8 show different angles of flowers of the same age). No pappus is initiated in this species, although other species in the genus do display various pappus forms. Figure 9 and Figure 12 depict the mature disk flower at anthesis (achenes have been detached). Clearly seen is the unusual structure of the disk style (Figs. 12, 13), characteristic of this tribe. The style is composed of two parts, the lower filamentous portion which is glabrous (Fig. 13, arrowhead labelled L), and the upper, wider portion which is covered with short trichomes (Fig. 13, arrowhead labelled U). The trichomes serve as a brush to pick up pollen (Figs. 10, 11) as the style elongates past the inwardly dehiscing stamens (S in Fig. 12), presenting the pollen to pollinators by the "brush mechanism" of Leins and Erbar (1990).
72. Venidium fastuosum
Ray flower—Ray flower primordia are difficult to distinguish from the disk flower primordia but for their slightly angular outline (R in Fig. 14). The involucral bracts may be identified by their upturned, flattened shape with acute tips (I in Fig. 14). Four, or rarely five, stamen primordia appear (Fig. 15, flower on left labelled S) after delimitation of an irregularly shaped corolla ring meristem (RM in Fig. 15). The stamen primordia continue to expand as the abaxial and lateral portions of the ray flower corolla begin to elongate zonally (Fig. 15, flower on right). The two carpels have been initiated and have begun to expand (Fig. 16, arrowheads labelled G). The anther portion of stamen primordia (A in Fig. 16) is delimited and a filament becomes evident (Fig. 17, arrowhead). The stamens are not aborted and continue to elongate during development (Fig. 18), but never develop to the stage of microsporogenesis and thus are evident only as small staminodia in the mature ray flower (Fig. 19, arrowheads).
73. *Venidium fastuosum*
Following Cassini's (1817) conclusions, Dittrich (1977) divided the Cynareae into three subtribes: the Echinopeae, Carlineae, and the Cardueae. The Cardueae are further subdivided into two lines, the Carduinae and the Centaureinae. Leins and Gemmeke (1979) studied the inflorescence and floral development in *Echinops exaltatus* of the Echinopeae, documenting the secondary aggregation of heads in the species, later confirmed by Petit (1988). In my study, *Centaurea maculosa* was examined as an example of the Centaureinae line in the Cardueae subtribe. *Carduus nutans* was examined as an example of the Carduineae line in the Cardueae. Finally, *Xeranthemum annuum* was examined as a member of the Carlinae subtribe.
Carduus nutans L.

"Musk or nodding thistle" collected in a fallow field in Bradley County, Tennessee.

Organogenesis sequence: Co, P, S, G

Scale: Bars in Figures: 1, and 7-14 = 50 \( \mu m \)

Bars in Figures: 2-6 = 500 \( \mu m \)

This biennial thistle displays a tall, robust, very prickly main axis with side branches of only one order. The main axis and each branch axis are terminated by a single inflorescence. Each inflorescence contains from 120-180 actinomorphic flowers. There are no differentiated peripheral flowers (rays) in this species.

Inflorescence--The inflorescence apex of Carduus nutans prior to flower initiation is broad and low-domed (Fig. 1). The heads are homogamous, and the bisexual flowers are initiated in the standard fashion in the family, beginning with the outermost and proceeding centripetally (Fig. 2). Floral initiation of additional flowers proceeds until the inflorescence apex is covered with primordia (Fig. 3, polar view of inflorescence). The progression of organogenesis on the head is acropetal, following the pattern of floral
74. Carduus nutans
initiation, beginning with the outermost flowers (Figs. 4, 5). At mid-development, the numerous pappus members and receptacular outgrowths obscure almost entirely the individual flowers (Fig. 6, half an inflorescence).

**Flower**—After initiation, the oldest, outermost flower primordia are directly subtended by the uppermost involucral bract primordia (F, I in Fig. 7). Above the level of the peripheral flower primordia, the remaining primordia do not have subtending involucral or receptacular bracts (Fig. 7, upper right, Fig. 8). The primordia pass through the plug stage (Fig. 8), before displaying the formation of five corolla lobe primordia (C in Fig. 9) without an intervening corolla ring meristem stage. Appearing soon after the corolla lobe primordia and alternating with them, the pappus arises as several individual primordia (P in Fig. 10). After initiation of five stamens (Fig. 11, removed, but scars labelled S) two carpel primordia are initiated (G in Fig. 11, flower same age as in Fig. 12). In mid-development the terminal appendages of the stamens can be seen (Fig. 13, arrowheads). The corolla tube will make up approximately half of the length of the corolla (Fig. 14, dividing line with the tube, CT, below, and the free corolla lobes, C, above).
75. Carduus nutans
Centaurea maculosa L.

"Spotted Knapweed", collected in an open field in Rockbridge County, Virginia.

Organogenesis sequence: Disk: Co, S, G, P  Ray: Co

Scale: Bars in Figures 1-5 and 8-22 = 50 µm
Bars in Figures 6-7 = 500 µm

Spotted knapweed is a loosely branched biennial with each of the numerous branches terminated by a head. The heads are uniform with about 50 central actinomorphic flowers, and about 15 peripheral flowers that are zygomorphic.

Inflorescence--In this species and genus (Dittrich, 1977), sterile peripheral flowers with spreading corollas are produced in the same manner as the true ray flowers found in the subfamily Asteroideae. Before initiation of any floral primordia, the inflorescence apex is highly domed (Fig. 1). The bisexual disk flowers are the first floral primordia evident on the surface of the inflorescence meristem (D in Fig. 2), leaving patches of uncommitted meristematic tissue at the base of each parastichy (Fig. 2, arrowheads). By the time all of the disk flowers have been initiated, the triangular ray flowers have also appeared (Fig. 3, arrowheads). After the primordial
76. *Centaurea maculosa*
plug stage (Fig. 3), organogenesis begins at the periphery of the head (Fig. 4) and proceeds rapidly, evidenced by the near synchronicity of stages in Figures 4 through 6. The ray flowers lag behind the disk flowers in corolla formation to some extent (D, R in Figs. 5, 6), but in late stages of development (R in Fig. 7) have caught up to the disk flowers (D) in size. Receptacular outgrowths are not evident until mid-development (Fig. 6, arrowheads), and so are not homologous to receptacular bracts (palea) in terms of initiation time.

**Disk flower**—After acropetal initiation of the more or less rounded disk flower primordia along shallow parastichies (D in Fig. 8), disk flower primordia pass through the plug stage quickly to form the five corolla lobes almost simultaneously (C in Fig. 9). Five stamen primordia are initiated next, seemingly simultaneously (Figs. 10, 11, same flower, arrowheads). After a period of growth and differentiation, the two carpel primordia (G in Fig. 12) can be distinguished, along with a pappus ring meristem (Fig. 12, arrowheads) at the summit of the ovary. Individual pappus member primordia do not appear until the style has elongated, elevating the carpel apices (Fig. 13, pappus members-arrowheads, style-T, carpel apices-G). In mid-development, two series of pappus members can be seen per flower (Fig. 14, arrowheads), and corolla trichomes have begun to differentiate.

**Ray or peripheral flower**—Ray flower arise as triangular primordia between the disk flower and involucral bract primordia (R, D, I in Fig. 15). The ray primordia expand (R in Fig. 16), and then flatten apically (R in Fig. 17). Although the ray flower primordia retain their roughly triangular shape, a full complement of five corolla lobe primordia is initiated (Fig. 18, flower on left with arrowheads), but only three of
77. *Centaurea maculosa*
78. *Centaurea maculosa*
these, the two laterals and the abaxial, will expand noticeably
(Fig. 18, flower on right, Fig. 19). No other organs are initiated
(Fig. 19, flower on left) even in mid-development (Fig. 20,
same age as in Fig. 21). Though the disk flowers are initiating
pappus primordia (Fig. 22, arrowhead labelled D), the rays do
not (Fig. 22, arrowheads labelled R).
Xeranthemum annuum L.

"Everlasting", grown from commercially available seed in the greenhouse, native to the Mediterranean.

Organogenesis sequence: Disk: Co, S, P, G Ray: Co, G, (P)

Scale: Bars in Figures 1-2 and 7-24 = 50 μm
Bars in Figures 3-6 and 25 = 500 μm

Xeranthemum annuum is a trailing herbaceous plant that may flower profusely. The heads are terminal and are borne singly on somewhat trailing side branches. The size of the heads varies, at least in the cultivar examined, with 16-65 bisexual actinomorphic flowers and 9-20 sterile peripheral flowers. While the number of flowers per head varies on a single plant, inflorescence and floral developmental events remained constant.

Inflorescence: Xeranthemum annuum also displays peripheral flowers, but they are more filamentous in nature and not as spreading as in Centaurea maculosa. The bare inflorescence meristem in this species is moderately domed (Fig. 1), and the disk flower primordia are all subtended by bracts that arise as a common meristem of disk flower primordium and bract primordium (D, B in Fig. 2). The bracts that subtend the
79. Xeranthemum annuum
outermost rows of disk flowers may be termed involucral bracts (phyllaries), and the more acropetal bracts receptacular bracts (palea), but they are initiated in continuous succession and at maturity there is a gradation in form. Thus, they are homologous structures, differing only in placement on the head. The distinction of involucral versus receptacular bracts does not apply here. Ray flower primordia are initiated in the remaining meristematic areas around the base of the inflorescence (R in Fig. 2), also with subtending bracts (removed in Fig. 2). After all the flower primordia have been produced on the inflorescence, organogenesis begins with the outermost disk flowers (Fig. 3). The flower primordia rapidly outstrip their subtending bracts in size (Fig. 3, arrowheads labelled B), obscuring the bracts until late development (Fig. 6, arrowheads labelled B). The ray flowers lag in development (Figs. 3-6, arrowheads labelled R), as the disk flowers undergo organogenesis and development in acropetal order (Figs. 4, 6).

**Disk flower**--After the bifurcation of the disk/bract common primordia (Fig. 2), the uppermost portion enlarges into the disk primordium proper (Fig. 7). Rapidly moving through the plug stage, the disk flowers form five corolla lobes apically and simultaneously (C in Fig. 8). The five stamens are then initiated next, sequentially in an irregular pattern (Fig. 9, arrowheads). The initiation event is quick enough so that the stamen primordia are all of equal size (Figs. 10, 11). Soon after the appearance of the stamen primordia, the first evidence of the pappus scales may be seen on the flanks of the flower as low swellings which are not circumferential (Fig. 11, arrowhead). As the stamens and the corolla lobes expand, the individual pappus primordia may be distinguished (Figs. 12, 13 same age flowers, arrowheads). Shortly thereafter, two carpel primordia are initiated, often at an oblique angle to a radius of the head rather than both lying on the radius (Fig. 4,
80. Xeranthemum annuum
arrowhead, G in Fig. 14). During mid-development, the apical stamen appendages (S in Fig. 6) and the developing style often protrude from the corolla lobes (Figs. 15, 16, 6). The acute pappus lobes are visible in Figures 16 and 25.

Ray or peripheral flower--As the early initiatory events for the peripheral flowers in this species are, for all purposes, identical to ray flower initiation seen in the Asteroideae, the peripheral flowers described here are simply termed ray flowers. At the base of each disk flower parastichy an uncommitted meristematic space is subtended by a bract primordium (Fig. 17, arrowheads). A triangular ray flower primordium is initiated in these spaces (Fig. 18, arrowheads). The primordium elongates (Fig. 19), and a slightly compressed corolla ring meristem forms around the periphery of the primordium (Fig. 20) that will become the corolla. One (rarely two) stamen primordium/a is briefly in evidence (S in Fig. 21) usually in the adaxial position, but is aborted and resorbed leaving no relictual structure (Figs. 22, 23). Two carpel primordia are initiated and are oriented perpendicularly to the radial plane of the head (G in Fig. 22). This perpendicular formation persists, as seen in the orientation of the cleft that forms the two stigmatic branches (Figs. 23-25). Portions of the corolla enlarge more than others, randomly forming lobes (Figs. 23-25) that do not elongate as quickly as the style and thus never cover or protect the interior of the flower. A pappus is rarely present in the ray flowers, but when expressed is similar to that of the disk flowers (Fig. 24, arrowhead).
81. *Xeranthemum annuum*
Tribe: Lactuceae (Cichorieae)

As summarized by Tomb (1977), a thoroughly satisfactory subtribal treatment of this family is not yet available. Stebbins (1953) and Jeffrey (1966) have presented the most recent schemes of tribal classification. The species chosen for examination are presented below, along with their subtribe (Stebbins, 1953), group and subgroup (Jeffrey, 1966) designations.

<table>
<thead>
<tr>
<th>Species</th>
<th>Subtribe</th>
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<td>Crepidinae</td>
<td>Tolpis</td>
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<tr>
<td>Cichorium intybus</td>
<td>Cichorinae</td>
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<td>Malacothrix saxatilis</td>
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<td>Pyrrhopappus carolinianus</td>
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<td>Tolpis barbata</td>
<td>Cichorinae</td>
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Andryala pinnatifida Aiton

"Andryala", collected from the University of California at Berkeley Botanical Garden. This species is native to the Canary Islands.

Organogenesis sequence: Co, P, S, G

Scale: Bars in Figures 1, 2 and 7-12 = 50 μm

Bars in Figures 3-6, 13 = 500 μm

Andryala is a stout much-branched semi-woody perennial plant. The heads are all ligulate, and occur in loose cymose synflorescences at ends of the branches. Eighty to 120 yellow ligulate flowers are present on a head.

Inflorescences—The inflorescence meristem is rather low-domed prior to floral initiation (Fig. 1). Occasionally, a young inflorescence meristem bifurcates unevenly (Fig. 1, arrowhead), to form two unequal inflorescence meristems. Both enlarge and undergo normal development. Flower primordia are first initiated on the periphery of the inflorescence meristem (Fig. 2) and proceed centripetally (Fig. 2) in parastichies, to fill the inflorescence meristem (Fig. 3, polar view). Organogenesis of the floral primordia begins on the periphery (Fig. 3, arrowheads), proceeding centripetally.
82. Andryala pinnatifida
(Fig. 4). By mid-development (Fig. 5), the flowers have become more or less equalized in size. Later (Fig. 6, half an inflorescence), the flowers have become totally equalized.

**Flower**--The flowers are initiated as low-domed primordia (Fig. 2) and rapidly expand to the plug stage (P in Fig. 7). The five corolla lobes are the first organs to appear (Fig. 8) and are initiated sequentially (Fig. 8, numbered lobes) in an irregular helical pattern. The next organ to appear is the pappus in the form of a ring meristem (Fig. 9 and 10, arrowhead labelled P) encircling the flower below the corolla. After the appearance of the pappus ring meristem, the stamen primordia begin initiation (Figs. 9 and 10, unlabelled arrowheads) in an irregular helical sequence. The corolla lobes expand and the corolla tube begins to elongate by zonal growth (C and CT in Fig. 11) while the individual pappus member primordia differentiate from the pappus ring meristem (Fig. 11, arrowheads labelled P). At about the same time, the two carpel primordia are initiated (G in Fig. 12). At mid-development (Fig. 13), the young achene is relatively short and longitudinally ridged. The adaxial slit in the corolla along which the ligule unfurls is also evident (Fig. 13, arrowhead).
83. Andryala pinnatifida
"Chicory", collected from a disturbed site outside of Lexington, Virginia.

Organogenesis sequence: Co, S, G, P

Scale: Bars in Figures 1-4, and 7-14 = 50 μm

Bars in Figures 5, and 6, = 500 μm

Chicory is a widespread weedy species with blue ligulate heads. The plant is minimally branched, and the heads are axillary along the axis. There are about 10-18 ligulate flowers on each head.

Inflorescence--The inflorescence meristem is hemispherical prior to floral initiation (Fig. 1); as development proceeds, the recpatacle flattens somewhat (Figs. 2-6) and is only slightly convex just before anthesis (Fig. 6). Flower primordia are initiated on the periphery of the inflorescence meristem (Fig. 2) and are more or less round. Initiation proceeds acropetally and uses up the inflorescence meristem. Organogenesis proceeds rapidly on the head, simultaneously for all flowers (Figs. 3-5). During early differentiation (Fig. 5), the corollas develop numerous trichomes (arrowheads labelled T). Glandular trichomes are present on the outer surfaces of the
34. Cichorium intybus
involucral bracts (unremoved bracts behind the head, Fig. 6, arrowhead labelled GT)

**Flower**—The flower primordia are initiated as low mounds (F in Fig. 7). Organogenesis begins quickly, without a noticeable plug stage (Figs. 2 and 3) or ring meristem. The five corolla lobes are the first organs to initiate (C in Fig. 8) and appear simultaneously without a preceding ring corolla stage. As the corolla lobes arch inward, the stamens are initiated more or less simultaneously (S in Figs. 9 and 10). A low ridge below the corolla tube encircling the flower primordium becomes evident (Fig. 10, unlabelled arrowheads). Two carpel primordia are initiated (G in Figs. 11 and 12). As the corolla tube elongates (CT in Fig. 13), numerous individual pappus member primordia differentiate (Fig. 13, arrowheads labelled P) at the top edge of the developing achene. These develop slowly (older stage, Fig. 14, arrowheads labelled P) to form numerous small scales at maturity (not shown).
85. Cichorium intybus
Malacothrix saxatilis (Nutt.) T. & G.

"Malacothrix" obtained from the collection of the University of California Botanical Gardens, at Berkeley. This species is native to California and grows in roadcuts and on sea bluffs.

Organogenesis sequence: Co, P/S, G

Scale: Bars in Figures 1-3, and 7-12 = 50 µm
Bars in Figures 4-6 and 14 = 500 µm

Malacothrix saxatilis is a perennial with several stems that are moderately branched. The numerous heads are terminal. Approximately 90 ligulate flowers are present on each head.

Inflorescence--The inflorescence meristem of this species is low-domed prior to floral initiation (Fig. 1). Flower primordia are initiated on the periphery (Fig. 2) and further floral initiation takes place centripetally (Fig. 3). Organogenesis as well begins with the peripherally located floral primordia (Fig. 4) and proceeds acropetally. In later stages of development (Figs. 5 and 6), the flowers equalize in size.

Flower--The floral primordia are initiated as low mounds (Fig. 2, arrowheads), generally with a rounded outline. The
86. Malacothrix saxatilis
87. Malacothrix saxatilis
primordia pass through the plug stage (PS in Fig. 7) rapidly. Organogenesis begins with the formation of the five corolla lobes in an irregular helical sequence (numbered corolla lobes in Fig. 7). The pappus primordia become evident next (Figs. 7 and 8, arrowheads labelled P) as five mounds roughly alternate with the corolla lobes. Each of the primordial sites will differentiate into several individual pappus members (Fig. 10, arrowhead labelled P), eventually filling in the gaps (Figs. 12-14, arrowheads labelled P). After the appearance of the initial pappus primordial bulges, the stamens are initiated (Figs. 8 and 9, arrowheads labelled S, and numbered stamens), in a sequential irregular order. The corolla lobes expand and arch inward (C in Fig. 10) before the two carpel primordia are initiated (Fig. 11, arrowheads labelled G). In later stages of development (Figs. 12-14), the corolla elongates by zonate growth (Z).
Pyrrhopappus carolinianus (Walter) DC.

"False dandelion", collected from a disturbed roadside site in Baton Rouge, Louisiana.

Organogenesis sequence: Co, S, P, G

Scale: Bars in Figures 1 and 2 = 50 μm
Bars in Figures 3-6, and 7-13 = 500 μm

False dandelion is an annual, tap-rooted species with several stems arising from the base of the plant. There are 3-5 heads on an axis, with the terminal head flowering first, and the axillary heads flowering in basipetal succession. There are about 120 ligulate flowers per head.

Inflorescence--The inflorescence meristem has a low dome (Fig. 1) prior to floral initiation. Flower initiation begins at the periphery (Fig. 2) and proceeds acropetally (Fig. 3). While the last flower primordia are being initiated at the summit of the inflorescence apex (Fig. 3), organogenesis begins in the outermost flowers (Fig. 3, arrowheads) with the appearance of the corolla. Organogenesis proceeds acropetally on the head (Fig. 4), and the flowers soon become essentially equalized (Fig. 5). During late stages of development, the involucral
88. *Pyrrhopappus carolinianus*
bracts develop prominent vertical wings (W in Fig. 6) that project upward.

Flower--After initiation (Fig. 2), the flower primordia rapidly develop into a plug stage (P in Fig. 7). Almost immediately, the five corolla lobes are rapidly initiated in an irregular helical pattern (see numbered corolla lobes in Fig. 7). After the corolla lobes are present, the five stamen corollas are initiated, also in an irregular helical sequence (Figs. 8-10, unlabelled arrowheads). After the stamens have all initiated, the pappus become evident as a low ridge encircling the flower below the corolla (Fig. 10, arrowhead labelled P). Numerous individual pappus member primordia differentiate (Fig. 11, arrowheads labelled P) from the ridge. At the same time, two carpel primordia are initiated (same flower, polar view, Fig. 12, arrowheads labelled G). In later development, the carpels have elongated more than the stamens (G and S in Fig. 13, and another series of pappus member primordia have differentiated (Fig. 13, arrowheads labelled P) below the original ring of primordia.
89. Pyrophopaprus carollinensis
*Tolpis barbata* (L.) Gaertn.

*Tolpis*, obtained from the collection of The Royal Botanical Gardens at Kew, Great Britain.

Organogenesis sequence: Co, S, G, P

Scale: Bars in Figures 1-5, and 8-15 = 50 μm

Bars in Figures 6 and 7 = 500 μm

*Tolpis* is a moderately branched annual with numerous terminal heads. There are about 100 ligulate flowers on each head.

*Inflorescence*--The inflorescence meristem has a low dome (Fig. 1) prior to floral initiation. Flower initiation begins at the periphery (Fig. 2) and proceeds acropetally (Fig. 3) to fill the head. Organogenesis begins in the outermost flowers (Figs. 3 and 4, arrowheads). Organogenesis proceeds acropetally on the head (Fig. 4), and the flowers soon become more or less equalized (Fig. 5) during mid-development. During late stages of development, numerous trichomes differentiate throughout the inflorescence (Fig. 6). In late stages, the corollas elongate and the head becomes flat-topped (Fig. 7).
90. Tolpis barbata
Flower--The flower primordia are initiated as low mounds (Fig. 8, arrowheads) and rapidly develop into a plug stage (P in Fig. 8). The five corolla lobes are rapidly initiated an irregular helical pattern (see numbered corolla lobes in Fig. 9). After the corolla lobes are present, the five stamen corollas are initiated, also in an irregular helical sequence (Fig. 10, unlabelled arrowheads). Two carpel primordia are initiated (Fig. 11, arrowheads labelled G) after the corolla has elongated somewhat and enclosed the rest of the flower (C in Fig. 12). Individual pappus primordia become evident along the upper rim of the achene (Fig. 13, arrowheads labelled P) after the carpels and stamens have elongated (G and S in the same flower, Fig. 14). At maturity, the achene is ridged and pappus forms a crown of bristles (P in Fig. 15).
91. *Tolpis barbata*
Tribe: Mutisieae

Cabrera (1977) recognizes four subtribes for the Mutisieae--the Barnadesiinae, Gochnatiinae, Mutisiinae, and the Nassauviinae. In the present study, the following taxa were examined from two subtribes: Acourtia runcinata, Trixis chiapensis, and T. inula (members of the Nassauviinae). Mutisia coccinea is a member of the Mutisiinae. Chloroplast DNA evidence suggests that the Barnadesiinae, a South American in distribution, are basal to the rest of the Asteraceae (Jansen 1990, and references therein). Living plants of Barnadesia caryophylla were obtained, but unfortunately have not flowered yet under cultivation.
Acourtia runcinata (D. Don) B. L. Turner

"Acourtia", collected roadside in Bee County, Texas.

Organogenesis sequence: Co/P, S, G

Scale: Bars in Figures 1,2 and 7-12 = 50 μm
Bars in Figures 3-6 and 13 = 500 μm

Acourtia runcinata is a perennial rosette that produces two or three heads per scape during the flowering season. There are 25-30 flowers on each head.

Inflorescence--The inflorescence meristem has a low dome (Fig. 1) prior to floral initiation. Flower initiation begins at the periphery (Fig. 2, arrowheads labelled F) and proceeds acropetally to fill the head. The outermost floral primordia arise in the axils of the uppermost involucral bract primordia (Fig. 2, arrowheads labelled B). Organogenesis proceeds rapidly in acropetal succession on the head (Figs. 3-4), and the flowers become completely equalized (Fig. 5) during mid-development. During late stages of development, the head is flat and the numerous pappus members elongate (Fig. 6).
92. Acourtia runcinata
Flower--After their initiation (Fig. 2, arrowheads labelled F), the flower primordia enlarge into the plug stage (Fig. 7). The corolla and the pappus appear at about the same time as in the form of irregularly located bulges (Fig. 8, arrowheads labelled C and P). The corolla lobes expand and individual pappus member primordia differentiate from the bulges (C in Fig. 9, arrowheads labelled P). The stamens are sequentially initiated (Fig. 10, arrowheads) on the sides of the concave floral axis, in an irregular order. Additional pappus members continue to differentiate below the older ones (Fig. 11-13, arrowheads labelled P). At the same time, the two carpels are initiated (Fig. 12, arrowheads labelled G) on a radial plane. Later in development the pappus all but obscures the corolla (Fig. 13).
93. Acourtia runcinata
**Mutisia coccinea** St. Hil.

"Mutisia", collected from a cultivated specimen obtained from the University of Michigan Botanical Garden. This species is native to the rain forests of Brazil in Minas Geraes, Sao Paulo and Parana states (Cabrera, 1965).


Scale: Bars in Figures 1, 7-20 = 50 µm

Bars in Figures 2-6 and 21 = 500 µm

**Mutisia coccinea** is a twining vine with numerous tendrils at the tips of the leaves. Heads are axillary and numerous. There are about 80 yellow disk flowers and 20 red ray flowers per head.

Infl orescence--The inflorescence meristem has a low dome (Fig. 1) prior to floral initiation. Flower initiation begins at the periphery and proceeds acropetally to fill the head (not shown). Organogenesis proceeds rapidly in acropetal succession, starting at the periphery (Fig. 2 and 3). The ray flower primordia are delayed only slightly in development (Figs. 3 and 4, arrowheads labelled R) compared to the neighboring disk flower primordia. By a later stage of development (Figs. 5 and 6), all of the flowers on the head have
94. *Mutisia coccinea*
equalized in size and the rays (Fig. 6, arrowheads labelled R) are practically indistinguishable from the disks.

**Disk flower**--The disk flower primordia rapidly expand to the plug stage (P in Fig. 7) and then form five corolla lobes in an irregular sequence (numbered lobes in Figs. 7 and 8). The pappus appears next as swellings below the corolla and alternate with the corolla lobes (Figs. 9 and 10, arrowheads labelled P). The stamen primordia initiate next (numbered stamens in Fig. 9) in an irregular sequence. The corolla lobes expand and arch inward, and numerous individual pappus members are differentiated from the earlier swelling (Figs. 11 and 12, arrowheads labelled P; same flowers). At the same time, two carpel primordia are initiated (Fig. 11, arrowheads labelled G); they are oriented somewhat randomly (i.e., not on the radial plane). Later, the carpels elongate (Fig. 13, arrowhead labelled G)

**Ray flower**--The meristematic areas on the inflorescence that gives rise to ray flower primordia are triangular in outline (Fig. 14, arrowhead). The ray flower primordia expand to the plug stage (P in Fig. 15) and are slightly smaller than the neighboring disk flower primordia (D). The five corolla lobes arise in an irregular sequence (Figs. 16 and 17, numbered lobes). Overlapping with the corolla initiation, the pappus is initiated as two lateral swellings below the corolla (Fig. 17, arrowheads labelled P). The swellings eventually encircle the flower completely (Figs. 18 and 19) and individual pappus primordia differentiate (arrowheads labelled P). Concomitantly, the corolla lobes have expanded (Fig. 18) to obscure the interior of the flower. Five stamen primordia initiate in rapid sequence alternate with the corolla lobes (S in Fig. 19). Two carpel primordia are initiated (Fig. 20,
95. Mutisia coccinea
96. Mutisia coccinea
arrowheads labelled G) at a random angle. Later, the ray flower is almost identical to the disk flower (D and R in Fig. 21); just before anthesis, the ray elongates greatly (not shown).
**Trixis chiapensis** C. Anderson

"Trixis", collected from a steep rocky roadcut in Chiapas, Mexico.

Organogenesis sequence: Co, P, S, G

Scale: Bars in Figures 1-3, and 7-12 = 50 μm

Bars in Figures 4-6 and 13 = 500 μm

**Trixis chiapensis** is a tall, moderately branched somewhat woody perennial. The numerous heads are terminal and are composed of bilabiate flowers only. There are usually about 15 flowers on each head.

**Inflorescence**--The inflorescence meristem is hemispherical before floral initiation takes place (Fig. 1). Involucral bracts are present and can be distinguished by their upcurved apices (Figs. 1 and 2, arrowheads labelled B). Flowers are initiated rapidly and acropetally (Fig. 2, arrowhead labelled F), some of them in the axils of the involucral bract primordia. Organogenesis begins with the peripheral flowers (Fig. 3, arrowheads) and rapidly proceeds in an acropetal direction. Soon, all the flowers become essentially equalized in stage and size (Figs. 4-6) and the receptacular trichomes become evident (Fig. 4, arrowhead labelled T). The numerous pappus
97. Trixis chiapensis
members and receptacular trichomes elongate during later stages (Figs. 5 and 6).

**Flower**—After floral initiation (Fig. 2) the flower primordia enlarge quickly, passing through the plug stage (P in Fig. 3), before corolla lobes are evident. The five corolla lobe primordia arise in an irregular sequence (Fig. 7, numbered lobes) and are immediately followed by the initiation of the pappus as a low bulge encircling the flower (Fig. 7, arrowheads labelled P). Rapidly, the corolla lobes and the pappus enlarge and differentiate (C and P in Fig. 8), the pappus forming numerous individual primordia (Fig. 8, arrowheads). The stamens initiate next (Figs. 9 and 10, arrowheads) in a rapid successive sequence. The first sign of carpel initiation is the appearance of a groove (Fig. 11, arrowhead) that separates the two carpels. The carpels elongate and become appressed (Fig. 12, arrowheads labelled G) slightly later. The two adaxial corolla lobes elongate to form the two-toothed lip, and the lateral and abaxial corolla lobes elongate to form the three-toothed lobes. The sinuses between the pair of abaxial lobes and lateral lobes are the deepest (Fig. 13). At anthesis, the two stylar branches (Fig. 13, arrowheads labelled Sb) protrude from the connate anthers (A), and the bilabiate corolla can be seen.
98. Trixis chiapensis
Trixis inula Crantz

"Trixis", collected roadside in Veracruz, Mexico.

Organogenesis sequence: Co, P, S, G

Scale: Bars in Figures 1-5, and 7-13 = 50 μm

Bar in Figure 6 = 500 μm

Trixis inula is a tall, moderately branched perennial. The numerous heads are terminal and are composed of bilabiate flowers only. There are usually about 9 flowers on each head.

Inflorescence--The inflorescence meristem is hemispherical before floral intiation takes place (Fig. 1). Involucral bracts are present and can be distinguished by their upcurved apices (Figs. 1, arrowheads labelled B). After initiation (not shown) the flower primordia undergo a plug stage (Fig. 2). Organogenesis takes place more or less simultaneously on the head (Figs. 3-5) and all the flowers are completely equal in stage and size (Figs. 4-6). The receptacular trichomes become evident as they protrude from the center of the receptacle (Figs. 4 and 5, arrowhead labelled T).
99. Trixis inula
**Flower**—Flower primordia rapidly pass through the plug stage (P in Fig. 7), before corolla lobes are evident. The five corolla lobe primordia arise in an irregular sequence (Fig. 8, numbered lobes) and are immediately followed by the initiation of the pappus as a low bulge encircling the flower (Fig. 9, arrowheads labelled P). Rapidly, the corolla lobes and the pappus enlarge and differentiate (C and P in Fig. 10), the pappus forming numerous individual primordia (Fig. 10, arrowheads). The stamens initiate next (Fig. 11, arrowheads) in a rapid sequence. The two carpel are initiated (Fig. 12, arrowheads labelled G) with a groove separating them (Fig. 12, arrowheads labelled Gr) that separates the two carpels. Later in development, the numerous pappus members elongate and obscure the corolla (Fig. 13).
100. *Trixis inula*
Tribe: Vernoniieae

At present, no satisfactory comprehensive treatment exists at the subtribal level for the tribe (Jones, 1977). The tribe has two centers of distribution, in the New World and in tropical Africa (Jones, 1977, and references therein). Of the roughly 1500 species in this tribe, about 1000 belong to the genus *Vernonia*; *Vernonia baldwinii* was chosen as a subject for the present study. *V. baldwinii* represents the New World line, and the other species chosen for examination, *Erlangea rogersii*, is of African origin. All species of this tribe have discoid heads; no ray or other peripheral flowers are found on the heads.
Erlangea rogersii S. Moore

"Erlangea", collected from the University of California at Berkeley Botanical Garden. Seed was originally obtained from Kirstenbosch Botanical Garden in South Africa.

Organogenesis sequence: Co, S/P, G

Scale: Bars in Figures 1-6, and 8-14 = 50 μm

Bars in Figures 7 and 15 = 500 μm

Erlangea rogersii is a tall (2-3 m) minimally branched perennial. There are roughly 10-20 discoid heads on an individual plant; the heads are arranged in terminal branched corymbs on the main and secondary axes. Each head is composed of roughly 35 actinomorphic disk flowers.

Inflorescence--Prior to floral initiation, the inflorescence meristem is hemispheric (Fig. 1) and subtended by inflorescence bracts (l). The hemispheric shape is evident in the early stages of inflorescence differentiation, as the flower primordia begin to initiate acropetally (Fig. 2), and after all flower primordia are present (D in Fig. 3). The receptacle flattens as development and differentiation proceed (Figs. 4-7). Organogenesis begins with the outermost and oldest flower primordia (Fig. 4) and rapidly proceeds in an
101. Erlangea rogersii
acropetal direction on the head. After organogenesis has begun
(Fig. 4), all the flower primordia rapidly become nearly
synchronized in stage of development (Fig. 5-7). By mid-
development (Fig. 7), while the flowers expand and trichomes
(arrowheads labelled T) differentiate, the receptacle is almost
entirely flat.

**Flower**--The flower primordia are initiated as low
protuberances on the meristematic surface of the
inflorescence (Fig. 2) and then expand into rounded plug shapes
(Fig. 8, arrowhead). It appears that the five corolla lobe
primordia arise separately on the flanks of the floral
primordium. No corolla ring meristem was seen. The
individual lobes appear in quick succession, not simultaneously
(Figs. 8, 9, numbered corolla lobe primordia). Asterisks
indicate positions that have not yet been filled with a corolla
lobe. The corolla lobes expand (Figs. 10, 11, numbered corolla
lobes), initially retaining a size differential that indicates
their order of initiation. Initiation of the corolla lobes is
not strictly helical; it appears to be more irregular, similar to
the non-helical sequence of sepal initiation reported for
several species of the Campanulaceae-Lobeliaceae (Erbar and
Leins, 1989). As the corolla lobes are expanding, the stamen
primordia are also being initiated in rapid succession (Fig. 11,
arrowheads). At the same time, protrusions arise on the sides
of the developing flower, the first evidence of pappus
primordia. The first pappus primordia to appear are located
more or less alternate with the expanding corolla lobes (Fig.
12, arrowheads). More pappus members are initiated as the
flower differentiates (Figs. 14, 15, arrowheads) to produce a
ring of bristle-like pappus members at maturity. The two
carpels are the last organs to appear (G in Fig. 13), after the
corolla tube has elongated substantially (CT in Fig. 14). Later
in development the flowers become incurved distally (Fig. 15)
102. Erlangea rogersii
due to the combination of crowding and pressure of the involucral bracts. At anthesis (not shown) the corollas expand with no noticeable distortion from the crowding.
**Vernonia baldwinii** Torr.

"Ironweed", collected on roadside along a limestone ridge in Franklin County, Missouri.

Organogenesis sequence: Co, P, S, G

Scale: Bars in Figures 1-4 and 7-13 = 50 μm

Bars in Figures 5-6 = 500 μm

Ironweed is an attractive perennial herb most commonly seen growing on the roadside, or in other disturbed sites. The main axis is usually unbranched below the terminal flat-topped corymbiform cyme. There are numerous (200+) discoid heads in each synflorescence, each with 25-35 purple flowers.

Inflorescence--Unlike *Erlangea*, the inflorescence meristem of *V. baldwinii* is almost flat (Fig. 1) prior to flower initiation. Flower primordia first arise on the periphery and then continue initiation centripetally (D in Fig. 2). Flower primordia may be distinguished from involucral bract primordia by shape: flower primordia are rounded, while involucral bract primordia rapidly become incurved and apically acute. By the time all of the flower primordia are present on the head, the receptacle is entirely flattened (Fig. 3). Organogenesis in the flowers begins with those flowers located peripherally and proceeds
103. Vernonia baldwinii
centripetally and rapidly on the head (Fig. 3). All of the flowers become more or less synchronized (Fig. 4). By the time organogenesis is complete, the flowers in the center of the head are indistinguishable in size and developmental stage from the peripherally positioned flowers (Fig. 5). During mid-developmental stages, the many bristle-like pappus members elongate (Fig. 6).

**Flower**—Flower primordia are first evident as low mounds (Fig. 2). They rapidly enlarge to the plug stage of development (Fig. 7, primordium labelled PS). This stage does not persist unchanged for long; the five corolla lobe primordia are initiated around the upper edges of the flower primordium. The corolla lobe primordia appear in rapid succession, (Fig. 7, flower primordia with numbered corolla lobes), without a preceding ring meristem stage. It is difficult to ascertain the sequence of initiation for the corolla lobes. Some flowers appear to adhere to a helical plan, while others show irregular order. Alternate to and just below the corolla lobe primordia, the first pappus primordia become evident as five bumpules (Fig. 8, arrowheads). Stamens are the next organs to be initiated (S in Fig. 9, one partially removed) after the corolla lobes have expanded and curved inwards (Fig. 10, same flower and others of same size). More pappus primordia have also been initiated (Fig. 10, arrowheads) between the five original sites. As the pappus members and the stamen primordia elongate (P, S in Fig. 11), two carpels are initiated (G in Fig. 12, same flower) on the radial plane of the head. Although the abaxial carpel primordium appears larger than the adaxial carpel and overarches it, the carpels become equalized (Fig. 12, arrowhead labelled G) by mid-development when the style begins to elongate (Figs. 12 and 13, arrowhead labelled St).
104. Vernonia baldwinii
Outgroup Taxa

Several families have been proposed as the sister group to the Asteraceae (Cronquist 1955, 1977; Bremer, 1987 and references therein). Of the many groups suggested in the literature, taxa from three families were chosen for investigation in the current study: Lobeliaceae, Goodeniaceae, and Calyceraceae. All flowers in the three families are basically pentam erous, sympetalous, and epigynous.
Calycera herbacea Cav.

"Calycera", collected from a disturbed, flooded area in Region del Maule, Provincia Talca, Chile

Organogenesis sequence: Co/P, S, G

Scale: Bars in Figures 2, 3, 5 and 8 = 50 μm

Bars in Figures 1, 4, 6, and 7 = 500 μm

Calycera herbacea is a low trailing perennial with numerous spherical heads arising on short peduncles from the axils of the leaves.

A complete ontogeny was not obtained for this species. The inflorescence seems to be of a condensed nature (Figs. 1 and 4), much like the inflorescence described for the Asteraceae species Gundelia tournfortii by Classen-Bockhoff et al (1989). The earliest floral stage available was of the corolla lobe initiation on the floral primordium (Figs. 2 and 3). The corolla lobes are initiated in a 2/5 spiral sequence (numbered lobes in Figs. 2 and 3). The sepals are initiated at the same time as the corolla lobes (Fig. 3, arrowheads labelled P), below and alternate with the corolla lobes. The next stage documented was of corolla expansion, the lobes arching inward (C in Fig. 5; flower on left partially dissected). The sepals do not enlarge
105. Calycera herbacea
appreciably (Fig. 5, arrowheads labelled P). At maturity (Fig. 6, arrowheads labelled P) they are little more than scales on the achene. The corolla lobes are equal (C in Fig. 7) in length to the stamens (S), while the style protrudes (St). The abaxial surface of the corolla displays numerous guard cells (Fig. 8).
*Calycera leucanthema* (Poepp. ex Less) O. Ktz.

"Calycera", collected roadside from a disturbed area in Region del Maule, Provincia Vilches Alto, Chile

Organogenesis sequence: Co, P, S, G

Scale: \( \mu \text{m} \) in Figure 20 = 5 \( \mu \text{m} \)

Bars in Figures 1-5, 8-18, = 50 \( \mu \text{m} \)

Bars in Figures 6, 7, and 19 = 500 \( \mu \text{m} \)

*Calycera leucanthema* is a low trailing herb with numerous spherical heads arising on short peduncles from the axils of the leaves.

**Inflorescence**—The ontogeny of the inflorescence and the individual floral groups were found to be similar to that described for the Asteraceae species, *Gundelia tournfortii* (Arctoteae) by Classen-Bockhoff et al. (1989). The inflorescence meristem is hemispherical before floral initiation (Fig. 1). Axillary cymes are initiated in acropetal sequence on the head (FG in Figs. 2 and 3) each subtended by a bract primordium (B) and uses up all the available meristem of the inflorescence (Fig. 4). A terminal flower primordium is initiated on the inflorescence and in each cyme (Fig. 5) and
106. Calycera leucanthema
smaller ones are initiated basipetally on each cyme. All of the axillary cymes are synchronized on the head (Figs. 5 and 6). In later development, the numerous bracts that subtend the individual flowers and the flower groups elongate markedly (B in Fig. 7).

**Cymose flower group**--The cymose flower group primordia initiate as elongate mounds (Fig. 8, arrowhead) while inflorescence bract primordia differentiate nearby (B in Fig. 8). The first flower primordium is initiated at the apex of the cyme primordium (Figs. 9 and 10, arrowheads labelled F), with small lateral lobes left uncommitted (L in Figs. 9 and 10). The lateral lobes enlarge to become additional floral primordia (L in Fig. 11) after the apical flower has begun organogenesis. Development follows this pattern (Figs. 12). The terminal flower of the inflorescence (Fig. 13) has several smaller flowers below it.

**Flower**--The floral primordia are initiated and expand into a plug-like stage (Fig. 10, arrowhead labelled F). The corolla lobes and the sepal lobes appear on the primordium at about the same time (Fig. 14, arrowheads labelled C and P). As the corolla lobes enlarge and arch inward (Fig. 15), the four stamens have initiated alternate with the corolla lobes. Two carpels are initiated (Fig. 16, arrowheads labelled G), with a small groove separating them. As the style elongates (Fig. 17, arrowheads) the distinction between the two carpels is obscured. The sepal primordia elongate (Fig. 18, arrowheads). At maturity, the style is exserted, and the sepals are stiff scales (Fig. 19, arrowheads labelled S). A single pendulous ovule (Fig. 19, arrowhead labelled O) is present in the achene. The abaxial surface of the corolla lobes displays numerous guard cells (Fig. 20).
107. *Calycera leucanthema*
108. *Calycera leucanthema*
Lobelia tupa L.

"Lobelia", obtained from the collection of the University of California Botanical Gardens, at Berkeley, California. This species is originally from Chile.

Organogenesis sequence: Sp, Co, S, G

Scale: Bars in Figures 2-17 = 50 μm
Bars in Figures 1, 18, and 19 = 500 μm

Lobelia tupa is a robust perennial plant with basal leaves and many tall inflorescences (to 2 meters). The flowers are located in racemes, and are deep red.

Inflorescence.—The inflorescence meristem is flat and produces numerous flowers and subtending bracts (Fig. 1), in a about a 5/8 helical phyllotaxy. Floral bracts are initiated at the inflorescence apex (B in Fig. 2), and floral primordia soon arise in their axils (Figs. 2 and 3, arrowheads). The floral primordia enlarge and elongate (Fig. 4), and organogenesis begins with the two adaxial sepals (Fig. 5, arrowheads). The two lateral sepals are initiated next (Fig. 6, arrowheads), and then the abaxial lobe last (Fig. 7, arrowhead). The corolla appears next, and is initiated as a pentagonal ring meristem
109. *Lobelia tupa*
(Figs. 8 and 9, arrowheads). The points of the pentagon enlarge rapidly to become the corolla lobes (Fig. 10, arrowheads) which immediately arch inward. The stamens are also initiated as a pentagonal ring meristem (Figs. 11, and 12, arrowheads). Again, the points of the pentagon enlarge to become the individual stamen primordia (S in Figs. 13 and 14) as the two carpels are initiated (Fig. 13, arrowheads) as two arcuate ridges that are separated by a wide gap. As development proceeds, the apices of the carpel elongate and grow toward each other (G in Figs. 15-17). During later stages of development, the carpel bases have undergone zonate growth (Figs. 18, 19, G). The ovules begin to initiate on the surface of the placenta meristem (Fig. 19, arrowheads labelled O). In the later stages, the flower displays a differential enlargement of the stamens, the first step toward the expression of zygomorphy (Figs. 18 and 19).
110. Lobelia tupa
111. Lobelia tupa
Scaevola calendulacea (Andr.) Druce

"Fanflower", material collected from cultivated plants at Davis, California. This species is originally from Australia.

Organogenesis sequence: Co, Sp, S, G

Scale: Bars in Figures 1-10, and the insert of 12 = 50 µm

Bars in Figures 11-14 = 500 µm

Fanflower is a creeping perennial herb, with blue fan-shaped flowers located in leaf axils.

The vegetative apex produces leaf primordia that are sub-opposite (VA and L in Figs. 1 and 2). Later, floral primordia are initiated (F in Figs. 1 and 2) in the axils of the leaf primordia. The flower primordia pass through a plug-like stage (Fig. 3) and then corolla lobe primordia are delimited on the apex of the floral primordium (Fig. 4, arrowheads) in sequence. Shortly thereafter, the sepals are initiated as bulges on the flanks of the floral primordium (Fig. 5, arrowheads). As development progresses, all five corolla lobes are evident (Fig. 6, arrowheads labelled C), retaining a size differential indicative of their sequential initiation. The sepals are also of slightly different sizes (Figs. 6 and 7, arrowheads labelled P). At the same time, five stamens are initiated (S in Fig. 7)
112. Scaevola calendulacea
alternate with the corolla lobes and apparently simultaneously. The corolla lobes expand and begin to arch inward (C in Fig. 8). Two carpel primordia are initiated as low arcuate mounds (Fig. 9, arrowheads labelled G) while the stamens enlarge. The apices of the carpels elongate (G in Fig. 10) and zonal growth below the lobes adds to the gynoecial height. As the style elongates (St in Fig. 11), the apex of the style broadens (arrowheads), the first evidence of the formation of the indusium that subtends the stigma at maturity (Fig. 14). The developing indusium has a clam-shape (Fig. 12, arrowheads). At this stage (Fig. 12), the sepals display guard cells on their abaxial surface (Fig. 12, inset). At maturity, the sepals are broad scales (Fig. 13, arrowheads) and the style is recurved downward toward the surface of the corolla (Fig. 14).
113. Scaevola calendulacea
LITERATURE CITED


Conclusions

Chapter 5
INTRODUCTION

Comparative ontogenetic studies of flowers are useful and significant at several levels. Morphological phenomena of early developmental stages of the inflorescence and the flower are documented at the most basic level. Particular structures are seen in early development of the inflorescence and flower, the significance of which has not previously been discussed for the Asteraceae. The ring meristem and occurrence of common primordia are important, and their varied manifestations have been studied and recorded in the current work.

At the next level, correlation and comparison of the morphological observations yields information about the inflorescence and floral developmental processes found in the Asteraceae. The evolutionary trends in development may then be assessed for the family.

Finally, phylogenetic conclusions may be drawn based on the distribution of the individual developmental characters among taxa and at different hierarchical levels. The family-wide occurrence of developmental trends is also recorded.

MORPHOLOGICAL PHENOMENA

Inflorescence--In those species examined that possess homogamous heads, floral initiation and subsequent development on the head are strictly acropetal/centripetal. This holds true for species in both subfamilies, for example:
Eupatorium fistulosum (Eupatorieae: Asteroideae) (Plate 25.2 and 3), and Carduus nutans (Cynareae: Lactucoeae) (Plate 74.2-4).

For all studied species with heterogamous heads, developmental phenomena occurring on the capitulum are partly acropetal (disk flowers) and partly basipetal (ray flowers). Species with so-called "true" ray flowers (apically three-toothed) typical of those found within the Asteroideae, consistently delay ray flower initiation until more acropetally located disk flowers have completed initiation. Subsequent development of the ray flowers is also delayed or suppressed; disk flowers always surpassed the ray flowers in both size and stage of development. Examples include Coreopsis tinctoria (Heliantheae sensu lato: Asteroideae) (Plate 31.15 and 16), and Senecio glabellus (Senecioneae: Asteroideae) (Plate 65.4-6).

Species in the Asteroideae with "filiform" flowers display similar phenomena. While initiation is acropetal for the filiform flowers of Gnaphalium purpureum (Inuleae: Asteroideae) (Plate 55.1 and 2), all the filiform flowers (excluding the larger, bisexual flowers) quickly become completely synchronized so that all on a head are of the same size and at the same stage of development (Plate 55.5). Some species with filiform flowers display bidirectional order of events (Fig. 1, p. 52). Rather than just a delay in initiation onset of a single series of primordia (or several series that eventually initiate subsequent primordia acropetally), filiform flower primordia are initiated in basipetal sequence from a non-peripheral starting point. The order from this point is bidirectional: while the filiform flower primordia are being initiated basipetally on the surface of the inflorescence meristem, disk flower primordia are initiated acropetally. Pluchea foetida (Inuleae: Asteroideae) (Plate 58.2 and 3), Erigeron philadelphicus (Astereae: Asteroideae) (Plate 2.7-10), and Eclipta alba (Heliantheae: Asteroideae) (Plate 35.2) show
bidirectional floral initiation. Development of the flowers on the head follows the same bidirectional pattern, with the largest and most developmentally advanced ray flower primordia located distally, and the most advanced disk flower primordia located proximally (plate 3.12).

Other peripheral flowers are found in species of the subfamily Lactucoideae. The tribe Arctoteae with well-developed "rays", is the most notable. The Calenduleae (Asteroideae), Chrysanthemoides monilifera (Plate 19.4-6), and Osteospermum fruticosum (Plate 24.21) have ray flowers that are apically three-toothed as are many ray flowers in the Asteroideae. Although not as pronounced, a delay in ray flower initiation and development is noticable during early stages of inflorescence differentiation. In the Arctoteae, Venidium fastuosum (Plate 71.2) shows a similar development, while Gazania longiscapa (Plate 68.2-3) also shows temporary suppression of the rays. The rays of Gazania develop differently (evident from the earliest stages of initiation) in that they regularly form two rather than three apical lobes (Plate 70.16-20). Peripheral or even ray flowers are also found in some genera of the Cynareae, and these display the same effects of suppression during early stages. Small, peripheral flowers are found in Xeranthemum annuum (Plate 79.4-6) that are delayed in initiation and development (Plate 81.17-20). The ray flowers of Centaurea maculosa (Plate 76.4-6) are entirely homologous in initiation and development to the ray flowers found in the Asteroideae. Ray flower primordia of Mutisia coccinea (Mutisieae: Lactucoideae) are delayed only slightly compared to the disk flower primordia during early development (Plate 94.2-6). Of all the species documented, the ray flowers of M. coccinea differ least from the neighboring disk flowers in symmetry and form (Plate 95.13) of all the species documented.
In general, the shape of the inflorescence meristem, just prior to floral initiation and during early stages of floral development, shows little tribal consistency or correlation to tribal boundaries. The myriad inflorescence forms found in the Heliantheae amply illustrate this (present study; see also Rauh and Reznik, 1953). Throughout the family, there is a tendency for species with homogamous heads to have flatter receptacles during early stages of floral initiation and development. For example, homogamous taxa such as Malacothrix saxatilis (Lactuceae: Lactucoideae) (Plate 86.2-4), and Liatris pycnostachya (Eupatorieae: Asteroideae) (Plate 27.1-6) have flatter receptacles than species with heterogamous heads, such as Centaurea maculosa (Cynareae: Lactucoideae) (Plate 76.1-5) and Rudbeckia laciniata (Heliantheae: Asteroideae) (Plate 49.1-6).

For a few more narrowly defined groups, some canalization (Stebbins, 1974) of inflorescence meristem shape can be seen. The inflorescences of those Inuleae with heterogamous heads are distinctly turbinate, as shown in Gnaphalium purpureum (Plate 55.2), and Pluchea foetida (Plate 58.1-3). Other species in this tribe with homogamous heads and the typical papery involucral bracts, including Helipterum roseum and Helichrysum bracteatum, also display the character, but to a lesser degree (see Plates 3-5 of Sharman and Sedgley, 1988). A conical inflorescence meristem appears to be a consistent character for the Calenduleae (Asteroideae) investigated: Calendula officinalis (Plate 17.1); Chrysanthemoides monilifera (Plate 19.1-3); and Osteospermum fruticosum (Plate 22.1-3) of the current study; see also Osteospermum vaillantii and Dimorphotheca pluvialis in Reese and Hilger (1984, Plate 2, a-c).

Flower--The Asteraceae possess several flower types (Leppik, 1977; Jeffrey, 1977) all of which are more or less related to each other morphologically. The main flower types
are mostly pentamerous or derived from a pentamerous condition, and include the following: the actinomorphic disk flower, usually bisexual; the bilabiate and ligulate flower, also bisexual; the ray flower; and filiform ray flower, the latter two flower types being either neuter or female. There are variations for each of these basic types involving sexuality, number of corolla lobes (or "teeth") expressed at maturity, and other phenomena involving some degree of organ suppression.

Comparative development of these floral morphs yields the significant conclusion that the early ontogeny of the disk flowers of the Asteroideae and that of the ligulate and bilabiate flowers of the Lactucoideae are almost identical. For disk flowers in the Asteroideae there is generally brief expression of a corolla ring meristem before the simultaneous differentiation of the individual corolla lobes, as seen in *Eclipta alba* (Heliantheae) (Plate 36.8 and 9). For bilabiate and ligulate flowers, a corolla ring meristem is generally not present prior to initiation of the corolla lobes, and the corolla lobes generally do not initiate simultaneously. Rather, an irregularly helical pattern or a merely nonsimultaneous initiation is observed for the corolla lobes of ligulate and bilabiate flowers, as in *Pyrrhopappus carolinianus* (Lactuceae: Lactucoideae) (Plate 89.7), and in *Trixis chiapensis* (Mutisieae:Lactucoideae) (Plate 98.7). It is almost impossible to distinguish any floral primordium as disk, ligulate, or bilabiate during early stages after the corolla lobes are present. The corolla of each morph achieves its recognizable form during mid-development and pre-anthesis expansion by the action of zonate or intercalary growth of the corolla tube. If the zonal meristem is intact below the level of corolla lobe attachment, a circular corolla tube typical of the disk flower forms. If the zonal meristem is not continuous, then the typical corolla of the ligulate flower, with one sinus, or of the bilabiate flower with two sinuses, results (see Figure 113).
Occasionally, the symmetry of disk flowers is altered, usually to a tetrameric state (excluding floral anomalies), possibly effecting a change in breeding system or reproductive output (Gardner, 1977). The tetrameric state may be consistently expressed (canalized) in all of the disk flowers on a head as in Coreopsis tinctoria (Heliantheae: Asteroideae) (Plate 29.3-6), or the expression may be erratic, suggesting a species uncanalized in regard to floral symmetry. Cacalia plantaginea (Senecioneae: Asteroideae) (Plate 61.5) and Galinsoga parviflora (Heliantheae: Asteroideae) (Plate 41.4-6) display both tetrameric and pentameric disk flowers randomly intermixed on a head.

The initiation and development of numerous ray flowers were documented in this study, for example, in Venidium fastuosum (Arctoteae: Lactucoideae) (Plate 73.14-19) and Tithonia rotundifolia (Heliantheae: Asteroideae) (Plate 54.13-19). In all cases, the primordia of the ray flowers has a triangular or otherwise bilateral shape from initiation onward. Depending on the number of corolla lobes initiated and the differential action of the corolla intercalary meristem, differing numbers of corolla lobes (apical teeth) are expressed in the development and final form of the ray flower limb. In Gazania longiscapa (Arctoteae: Lactucoideae), (Plate 70.16-20), two lobes are initiated; both persist during elongation and are present on the ray at anthesis. The ray flower primordia of Chrysanthemoides monilifera (Calenduleae: Asteroideae), (Plates 19.4-6, 21.15 and 16) initiate five corolla lobes, but only three, the two lateral and the abaxial, show basal intercalary growth, while the two adaxial corolla lobe primordia are suppressed. Four corolla lobes are initiated by ray flowers in Galinsoga parviflora (Heliantheae: Asteroideae) (Plate 43.14-16), again with the adaxial lobe or portion suppressed. The suppression of the adaxial lobe(s), along with the non-continuity of the intercalary meristem of the ray
corolla, produces the "slit" in the ray corolla. During late stages of development, the ray corolla may broaden considerably.

Despite the distorted shape of the developing ray flower primordium and other crowding-related mechanisms, stamen primordia are often initiated. Rarely are the relictual staminodial structures as noticeable in adult stages, as they are in *Chrysanthemoides monilifera* (Calenduleae: Asteroideae), (Plate 21.19), and *Dresslerothamnus* spp. (Senecioneae: Asteroideae) (Robinson, 1989). In some cases, only two stamen primordia are initiated, as in *Tithonia rotundifolia* (Heliantheae: Asteroideae) (Plate 54.16 and 17), and these are aborted and resorbed (Plate 54.18). *Chrysopsis camporum* (Astereae: Asteroideae) (Plate 16.18-20) typically has four stamen primordia initiated in each ray flower primordium. The ray flowers of *Mutisia coccinea* (Mutiseae: Lactucoideae) (Plate 96.19) regularly initiate five stamen primordia. Some species, such as *Rudbeckia laciniata* (Heliantheae: Asteroideae) (Plate 51.19-21), show no evidence of stamen or carpel initiation whatsoever.

Also occupying a peripheral position on the head are the filiform ray flowers, often present in several series. The primordia of these rays are always rounded and are measurably smaller than the bisexual disk flower primordia of the same head (see Table 3.1 on p. 51). The size of the filiform flower primordia seems to be genetically constrained, rather than limited by space consideration as are the ray flower primordia discussed above. *Pluchea foetida* (Inuleae: Asteroideae) (Plate 58.3) produces many filiform flower primordia that are initially well-spaced on the inflorescence surface. Stamen primordia were not noted during any stage in any of the filiform flowers examined in the current study; all are female, with the two carpel primordia occupying all of the space available in the interior of the flower, as in *Erigeron*
philadelphicus (Astereae: Asteroideae) (Plates 6.34, 35, 7.36-39). Corollas of the filiform flowers take one of two forms: either trimerous during early stages and showing three apical teeth at maturity, or bilateral, with no recognizable lobes or teeth. Gnaphalium purpureum (Inuleae: Asteroideae) (Plate 57.19), and Calendula officinalis (Calenduleae: Asteroideae) (Plate 18.13-15) both show examples of three corolla lobes in filiform flowers. Only the abaxial portion of the corolla ring meristem enlarges in the filiform flowers of E. philadelphicus (Astereae: Asteroideae) (Plate 7.36-38), an example of the type lacking teeth.

Female peripheral flowers were also noted in some members of the tribe Cynareae (Lactucoideae). The peripheral flowers in Centaurea maculosa are initiated similarly to a ray (Plates 76.2, 78.15, 16) and develop similarly as well (Plate 78.17-19). The only observed difference is the relative inactivity of a corolla intercalary meristem that is typically seen in later stages of corolla development in ray flowers. Of the five corolla lobe primordia that are initiated, three lobes elongate in mid- to late developmental stages, with little or no basal extension of the corolla (Plate 78.20 and 22). In Xeranthemum annuum, the corollas of the peripheral flowers are even more stunted (Plate 79.6); they are not noticable at maturity.

Other observations--Several other structures of particular interest were noted during early developmental stages. These include the phenomenon of a ring meristem, a widespread in the subfamily Asteroideae, but relatively uncommon in other families. A second feature to be discussed is the receptacular bracts which were seen to initiate in three different ways. The third phenomenon to be discussed is the initiation of the pappus, which is either integral with organogenesis or occurs later. Different patterns were recorded for the initiation of multiple pappus members.
A ring meristem was often documented in early organogenesis for the corolla, but only in the Asteroideae. Disk flower primordia in the plug stage develop a torus-shaped meristem apically, which is designated the corolla ring meristem; e.g. *Gnaphalium purpureum* (Inuleae) (Plate 56.8), and *Dyssodia tenuiloba* (Plate 33.7 and .8). The corolla lobes then differentiate directly from the ring meristem, usually simultaneously: *Anthemis cotula* (Anthemideae) (Plates 8.4, and 9.7), and *Eupatorium fistulosum* (Eupatorieae) (Plate 26.8). The corolla of filiform flower primordia also begins as a ring meristem, that is evident for a longer period than in the disk flower primordia: *Erigeron philadelphicus* (Astereae) (Plates 6.28-34 and 7.36), and *Calendula officinalis* (Calenduleae) (Plate 18.9). As the ring meristem is recognized primarily by its perfectly round shape, it is more difficult to ascribe this phenomenon to the ray flower corolla because of the more irregular initial shape of the ray flower primordium.

The presence of a corolla ring meristem initiated prior to the appearance of individual corolla lobes was documented by early anatomists (Koehne, 1869; Haenlein, 1874; Warming, 1876; Martin, 1892) All noted the presence of a "ringformigen Rand" or a "tubular ring" (Martin, 1892) as the first sign of organogenesis. Leins and Erbar (1987) depicted the corolla ring meristem, but failed to comment or identify the meristem as such, referring to it obliquely by the use of the term, "Trichterstadium" (or funnel-stage) to describe the entire floral primordium. Later, in a study of floral development in certain Campanulaceae, Lobeliaceae, Goodeniaceae, and Brunoniaceae (Erbar, 1987; Erbar and Leins, 1989), the term corolla ring meristem was employed to describe corolla initiation. The presence of a corolla ring meristem was documented for most of the species examined in the Asteroideae. Thus, the phenomenon of the corolla ring meristem has been well-documented by several workers and in
the current study, but has suffered an identity crisis in terminology up until this point.

Three different types of initiation for the receptacular bracts were recorded. Most commonly, the receptacular bract arises as part of a common primordium with a disk flower primordium. The common primordium is initiated as a large low mound that soon bifurcates: *Tithonia rotundifolia* (Heliantheae: Asteroideae) (Plate 53.6), and *Xeranthemum annuum* (Cynareae: Lactucoideae) (Plate 80.7).

The receptacular bract primordia may also be initiated individually after the appearance and some enlargement of the disk flower primordia. *Galinsoga parviflora* (Heliantheae: Asteroideae), (Plate 42.9), and *Madia elegans* (Heliantheae: Asteroideae), (Plate 46.2) both show delayed initiation of receptacular bracts. The bracts may also arise as enations initiated relatively late from the surface of the receptacle: *Chrysopsis camporum* (Astereae: Asteroideae) (Plates 14.5-6, and 15.12). These late appearing bracts do not regularly subtend the disk flowers and seem to arise where there is the greatest amount of space available on the receptacle. Therefore, the enation-type of receptacular bract is probably not homologous to the receptacular bract that is initiated integral with the subtended disk flowers.

Rarely, as in *Rudbeckia laciniata* (Heliantheae: Asteroideae) (Plate 50.7), is the receptacular bract initiated first, with the disk flower primordium appearing very soon thereafter in the axil of the bract.

Receptacular bracts are viewed as homologous to the subtending floral and/or inflorescence bracts found in a raceme (Cronquist, 1955, 1977). Those heads lacking receptacular bracts are considered more derived (Stuessy and Spooner, 1988). At maturity, the receptacular bracts (or palea) may take many forms in the Asteraceae (Stuessy and
the Asteraceae contains many references to a common primordium that bifurcates to produce the primordia of the disk flower adaxially and the receptacular bract abaxially (Marc and Palmer, 1978; Moncur, 1981; Gottlieb and Ford 1987; Sharman and Sedgley, 1988). This was also the most common pattern found for receptacular bract initiation in the current study. Evolutionarily, a common primordium of this type may have arisen as result of the condensation of the inflorescence axis from the raceme state to the head, as is found in the Asteraceae.

Initiation of the pappus was found to be either integral with organogenesis, as in *Accourtia runcinata* (Mutisieae: Lactucoideae) (Plate 93.8-10), or occurring late as enations around the summit of the ovary, as in *Eclipta alba* (Heliantheae: Asteroideae) (Plate 36.10-14), and *Cichorium intybus* (Lactuceae:Lactucoideae) (Plate 85.13-14). The mature forms of the late-occurring pappi were usually of scale, awn or crown types.

When pappus initiation is integral with organogenesis, three basic patterns emerge for the proliferation of the individual pappus members. Commonly found is the sequential initiation of numerous bristle-like members, beginning in five sites located alternately with the corolla lobes: *Senecio glabellus* (Senecioneae: Asteroideae) (Plate 66.10-11) and *Malacothrix saxatilis* (Lactuceae: Lactucoideae) (Plate 87.10-14). Additional pappus members are initiated sequentially, filling in the gaps from both sides.

Another type of pappus initiation appears as a random process, apparently subject to crowding pressures. In this pattern, the pappus member primordia are initiated wherever space is available. The crowding may be a result of the neighboring floral primordia as in *Mutisia coccinea* (Mutisieae: Lactucoideae) (Plate 95.10-12) and *Trixis inula* (Mutisieae: Lactucoideae).
Lactucoideae) (Plate 99.4). Pressure exerted from the involucral bracts may also cause the crowding effect: *Liatris pycnostachya* (Eupatorieae: Asteroideae) (Plate 25.4-6). Usually, by later stages of development, the sequential initiation of pappus members is all but obscured as all the bristles equalize.

The final recorded form of pappus initiation is the appearance of a pappus ring meristem, from which many individual pappus member primordia differentiate simultaneously. As illustrated for *Erigeron philadelphicus* (Astereae: Asteroideae), the ring meristem of the pappus (Plate 4.17-20) arises as a ridge that encircles the flower midway, from which individual pappus member primordia differentiate somewhat later (Plates 4.21-22, 5.23). Other species also display pappus ring meristems with simultaneous member differentiation, such as *Pluchea foetida* (Inuleae: Asteroideae) (Plate 59.9).

At this time, developmental trends in pappus initiation are undefined except for a few generalizations. The initiation of the pappus as a ring meristem with subsequent simultaneous differentiation of individual members is a more derived state than the other patterns discussed above that are integral with organogenesis. Pappus members that are initiated late in development as enations are not homologous to pappi initiated during organogenesis. Pappi of this nature seem to arise as outgrowths of the achene during differentiation rather than as an organ or organ whorl during organogenesis.

Events occurring early in the ontogeny of Asteraceae include phyllary initiation, initiation of flowers on the inflorescence meristem, organogenesis of the individual flower primordia, and establishment of floral symmetry. Early suppression of ray flowers frequently occurs after floral initiation, although the expression of this character is variable from one taxon to another. Other events occur at mid-development, such as organ
form differentiation, organ abortion (e.g., of anther primordia of the ray flowers), and the initial intercalary growth of the fused stamen/corolla tube. Some events that occur late, that is, shortly before anthesis, are final expansion of the corolla tube or ligule, and epidermal sculpturing and trichome development on such organs as the stigma, anther, filament and corolla of both the disk and ray flowers. The pappus may be initiated at any of various stages during floral development in different Asteraceae taxa, unlike the timing of calyx onset found in other families, wherein the calyx is always the first set of floral organs initiated.

EVOLUTIONARY TRENDS IN DEVELOPMENT

Uniformly acropetal initiation and development are correlated with a single flower type per head. Strictly acropetal development does not occur in species of the Asteraceae that possess heterogamous heads, as demonstrated by the taxa examined in the present study.

In heterogamous species of Asteraceae, a negative correlation exists between the degree of morphological similarity between the disk and ray flower primordia of a particular species and the duration of suppression of its ray flowers. The species with the most similar disk and ray flower primordia during early stages of development, Mutisia coccinea, displayed the least suppression of the ray flowers. The species with the most dissimilar flower morphs is Erigeron philadelphicus, with disk and filiform types; it has the most pronounced expressions of ray flower suppression, bidirectional floral initiation and development. Intermediate between these two extremes (Mutisia and Erigeron) are the species with typical ray flowers, in the Asteroideae, in which
the suppression is usually limited to a delay in initiation and subsequent development.

The present study suggests that the filiform ray flowers are more highly derived than the rays with triangular primordia. The filiform ray flowers display highly modified corollas (often lacking individual lobes), a total lack of individual stamen primordia during all stages of development, and the most pronounced suppression in both timing and development. Staminodial structures are frequently found in the typical ray flowers, although are often aborted and resorbed by maturity.

Compared to the central, bisexual flowers on the head, the peripheral flowers of the Cynareae are relatively small and unobtrusive. Initiation and early development are similar to those of the ray flowers found throughout the Asteroideae and in the Arctoteae. Later corolla expansion, resulting from an intercalary meristem, is absent in these flowers. Most of the expansion and differentiation of the characteristically showy ray flower ligule takes place during late stages of development, just prior to anthesis. The peripheral flowers of the Cynareae are homologous to typical ray flowers, but the rays possess additional terminal stages in corolla expansion.

The phenomenon of the peripherally located ray flower that varies in expression of symmetry, sexuality and corolla form is widespread throughout the Asteraceae. All of the ray flower forms described herein may be placed on a continuum. I suggest therefore that the term "true ray flower" as generally used by Bremer (1987), defined as apically three-toothed, and occurring exclusively in the Asteroideae, is inappropriate. As I have shown, only slightly modified ray flowers are found in the Arctoteae and the Cynareae. In addition, the corollas of many perfectly acceptable ray flowers, in both subfamilies, do not possess three apical teeth. Ray flowers, in the broader definition used here, are united by the occurrence of triangular or bilaterally shaped primordia and the consistent delay in
initiation and development as compared to disk flowers on the head. I define filiform ray flowers on the basis of their primordia, which are consistently round and small, have abbreviated corollas, and show complete loss of stamens. Within these two categories of ray flowers, the ray sensu lato and the filiform morph, subdivisions may be made based on 1) presence of corolla intercalary meristem, 2) number of corolla lobes, 3) number of stamen primordia initiated, and 4) in degree of suppression in timing of ontogenetic events. As discussed above, much growth and expansion of the ray corolla takes place during late stages of development, obscuring patterns and structures present in earlier stages. Thus, it is the expression of late-occurring morphological characters that are normally examined by systematists for comparative purposes of phylogeny assessment. By examining the canalized (Stebbins, 1974) floral characters, particularly those that occur earlier in development, it should be possible to demonstrate more clearly the pattern of parallel evolution of rays and the divergence of floral morphs in the Asteraceae.

The current study has shed new light on the nature and homologies of certain structures found in the Asteraceae, and these merit further discussion. The presence of a corolla ring meristem, and the initiation of receptacular bracts and pappus will be further examined.

PHYLOGENETIC CONCLUSIONS

It has been hypothesized that the timing of ontogenetic divergence between two taxa is positively correlated with the evolutionary divergence between taxa (Stebbins, 1974; Gould, 1977; Tucker, 1985). In other words, the earlier in ontogeny a character appears, the more canalized it is. Stages are added
terminally, gradually lengthening the ontogeny. Later stages, such as pre-anthesis elongation and differentiation, were probably added more recently (in evolutionary time), and are more easily modified. Early developmental stages of flowers and inflorescences are canalized and thus not as easily altered. Such canalized characters provide a firm basis for phylogenetic reconstruction. The ontogenetic method of phylogeny reconstruction is not without problems in application. The presence of non-terminal additions, deletions and of neoteny are much discussed in the literature (Nelson, 1978, 1985; Kluge, 1985; DeQueiroz, 1985) but seldom definitively documented, particularly for plant systems.

Inter-generic comparison--The most closely related taxa examined in the current study are two species in the genus Trixis. *Trixis chiapensis* and *T. inula* (Mutiseae: Lactucoideae) were chosen as clearly defined species of a generally accepted genus. The two species differ in vegetative characters, habit, and area of distribution (Anderson, 1972). Differences also exist in inflorescence and floral characters, such as the number of flowers on a head, and the length of various floral structures at maturity. As found in the present study, (Plates 97-100) the inflorescence and floral ontogenies of the two species are almost identical. Other than the number of flowers initiated, all of the separating floral and inflorescence characters develop during mid- to late stages of ontogeny, similar to the development seen in *Caesalpinia* (Tucker et al., 1985). This supports the hypothesis stated above; one would expect two species of a genus to have diverged more recently, and so to share a larger portion of a common ontogeny.

Higher level taxonomic comparisons--At a higher level, some developmental trends characterize certain tribes or tribal groupings. The synchronization of floral development on a head characterizes the species of the Vernonieae examined.
Of the pappus characters, the presence of the late-forming enations is mostly limited to the Heliantheae. The Astereae and the Inuleae both share the character of the pappus ring meristem that forms individual members simultaneously.

The distribution of ray flower primordia of different shapes throughout the family was meaningful. The ray flower primordia that show the most similarity to the disk flowers on the head belong to *Mutisia coccinea* (Mutisieae: Lactucoideae). Although the Mutisieae are not a monophyletic unit (Bremer, 1987), the subtribes are probably basal in Asteraceae phylogeny. One can conclude that the ray flower primordia of the Mutisieae are of a primitive nature compared to the ray flower primordia of the rest of the family.

Based on floral ontogenetic evidence, the delimitation between the two subfamilies seems to be somewhat unnatural because of the continuum of developmental characters observed. Aside from the primitive state found in *Mutisia*, there is a continuum of ray flower characters spanning the subfamilies. In particular, the rays of the Cynareae and the Arctoteae demonstrate that ontogenies are very similar to those found in members of the Asteroideae. The only characters separating the two subfamilies are: the presence of the corolla ring meristem, and the simultaneous initiation of stamens, both occurring in the majority of the Asteroideae examined. The Lactucoideae lack the corolla ring meristem and usually display an irregularly helical type of stamen initiation. These are early developmental characters that are strongly canalized.

**Outgroup comparison**—Of the outgroup taxa examined in the present study, none is presented here as the ancestral group to the Asteraceae; they are all highly derived along with the Asteraceae. The question is: Which living family shares the most recent common ancestor with the Asteraceae? By
examining the inflorescence and flower development, one can postulate the character states of the hypothetical ancestor of the Asteraceae, and determine the living sister family.

The inflorescence architecture of the Calyceraceae and Goodeniaceae is quite derived. *Calycera herbacea* and *C. leucanthema* both have inflorescences that are tertiarily condensed (Plates 105 and 106). This pattern is also recorded for a species of the Asteraceae, *Gundelia tournfortii* (Classen-Bockhoff et al., 1989), and is clearly a highly evolved synflorescence. The inflorescence of *Scaevola calendulacea* is spike-like but indeterminate (Plate 110), with single flowers in the leaf axils. When the plant is flowering, the floral primordia arise in the axils of the leaves fairly close to the vegetative apex. Neither of these inflorescence types, the indeterminate spike or the tertiarily condensed head, could have given rise to the head of the Asteraceae without many intermediate forms. However, it is not difficult to hypothesize a condensation of a racemose inflorescence such as that of *Lobelia tupa* (Plate 109.2) to bring about the capitulum of the Asteraceae (Erbar, 1987). The inflorescence apex of *Lobelia tupa* (Plate 109.1-2) already markedly resembles a flatter inflorescence meristem of the Asteraceae, similar to that found in *Tithonia rotundifolia* (Heliantheae: Asteroideae) (Plate 52.3). Thus, it seems clear that the ancestor of the Asteraceae had a racemose inflorescence.

While the inflorescence architecture has clearly diverged between the Goodeniaceae and the Calyceraceae and the Asteraceae, comparison of the structure and ontogeny of the flowers is productive. The ontogeny of *Lobelia tupa* flowers, despite being sympetalous and epigynous, is the least similar to the floral development found in the Asteraceae.

The floral ontogeny of the two *Calycera* species examined is similar to that of the Asteraceae in several ways. The calyx or pappus lobes are not initiated first--they appear soon after
the corolla lobes have differentiated (Plate 106.5). The stamens are initiated next, and finally, the two small carpel primordia (Plates 107.12 and 108.16) are initiated. As the carpels fuse and elongate, however, the integrity of the two carpels is lost (Plate 108.17) unlike the situation in the Asteraceae in which the apices of the two carpels eventually form the stylar branches. In addition, the Calyceraceae uniformly possess a pendulous ovule (plate 108.19) unlike the consistently basal ovule of the Asteraceae.

Based on the current study of comparative inflorescence and floral development, the Goodeniaceae appear to share the greatest amount of derived ontogenetic characters with the Asteraceae. However, some Goodeniaceous flowers do not show many early similarities with the Asteraceae. For example, the calyx and corolla initiation in *Selliera radicans* (Leins and Erbar, 1989) are strongly helical, and the floral primordium is apparently without a plug stage analog. In *Scaevola calendulacea*, examined in the current study, the development of floral primordia displayed several homologies to stages in the ontogenies recorded for the Asteraceae. The floral primordia, although axillary, pass through a plug-like stage (Plate 110.3-5) initially. As organogenesis begins, The corolla lobes and the calyx lobes are initiated simultaneously. The calyx lobes are not located terminally on the primordium; rather, they arise on the flanks of the floral primordium, closer to the base, much like the pappus in Asteraceae. The corolla lobes initiate in rapid helical sequence as bulges on the edges of the floral primordium, also in the manner of the Asteraceae. Two carpel primordia are initiated with a wide gap between them (Plate 112.9-10) that becomes the locule of the flower. During later stages of floral development, resemblance to the Asteraceae ends, especially when the indusium that subtends the stigma in the Goodeniaceae develops (Plate 112.12).
Thus, the Goodeniaceae seem a good candidate for sister group to the Asteraceae. This has been suggested in the past (Jeffrey, 1977), often in combination with other possible candidates. The ovule is basally attached as in the Asteraceae, but its often biovulate, and sometimes multiovulate, state has seemed an obstacle for those who have implied (Cronquist, 1977; Bremer, 1987) that the Asteraceae evolved from an ancestor that also possessed a single ovule.

SUMMARY

Comparative ontogenetic studies have been shown to be useful on different levels. Morphological phenomena have been documented that have not been recorded previously. Deviations from an overall acropetal course on the head are common in taxa having two floral types.

The formation of the ray flower of the Asteraceae shows three basic patterns of development: the ray flower *sensu lato*, the filiform ray flower, and the "*Mutisia*" type. The "*Mutisia*" type is considered the most primitive. Two tribes in the Lactucoideae, the Arctoteae and the Cynareae, display ray flower formation comparable to the patterns found in members of the Asteroideae.

Corolla ring meristems are generally present in Asteroideae species. The individual corolla lobes are differentiated to form the corolla ring meristem simultaneously. Receptacular bracts in the Asteraceae are usually initiated as common primordia in conjunction with disk flower primordia. The common primordium bifurcates and produces the receptacular bract abaxially and the disk flower primordium adaxially. The pappus may be integral with organogenesis, or may occur
during mid- to late stages of floral development. If the pappus is initiated during organogenesis, it may happen in one of three basic patterns; sequentially in five sites, as a ring meristem with simultaneously appearing individual members, or sequentially in a pattern dictated by crowding or packing pressures.

The two taxa with the most similar ontogenies were two species of the genus *Mutisia*. The findings support the hypothesis of the similarity of derived ontogenetic pathways to evolutionary divergence between two taxa. Groups within the Asteraceae can be characterized by certain developmental pathways. The presence of a corolla ring meristem and the simultaneous initiation of the stamens is confined to the subfamily Asteroideae. Certain tribes may also be characterized by particular developmental phenomena, such as the turbinate inflorescence meristems of the Inuleae.

The ancestor of the Asteraceae most likely had a racemose inflorescence. There are some references in the literature to either an occasional bi-ovulate ovary in *Lactuca sativa* (Jones, 1927), or to rudimentary septa in the achenes, possibly indicating a loss of a previously biloculate condition (Leins and Gemmeke, 1979; Hilger and Reese, 1983; Reese and Hilger, 1984). The Goodeniaceae are postulated as the sister group (ie. they share the most recent common ancestor) to the Asteraceae, based on floral development and placentation. The Calyceraceae are more closely related to the Goodeniaceae-Asteraceae complex than to the Lobeliaceae. Ontogenetic evidence suggests that the Lobeliaceae are only distantly related to the Asteraceae.
LITERATURE CITED


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**Society memberships**

Botanical Society of America

American Society of Plant Taxonomists

Sigma Xi
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Publications


**Publications in preparation**


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