Floral development of
Basella rubra L. (Basellaceae)

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ABSTRACT

Floral development of Basella rubra L.

The flower of Basella rubra L. poses two morphological problems: a) superposition of stamens and tepals, b) basal placentation. a) The first problem is a phyllotactic one. If we consider the classical definition of the flower (a modified monaxial shoot bearing fertile and sterile phyllomes), existing phyllotactic theories could be used to explain the arrangement of phyllomes on the floral axis. However, an investigation of the spatio-temporal pattern of tepal-stamen initiation shows that existing phyllotactic theories do not adequately explain the phenomenon of superposition. Hence, a change in phyllotactic theorizing and/or the interpretation of the flower appears to be necessary. b) The second problem concerns the carpel, which is traditionally defined as a folded phyllome that bears and encloses ovule(s). If this definition is applied to the gynoecium of B. rubra it is acarpellate because the single bitegmic ovule forms directly from the floral apex. If the term carpel is redefined as a gynoecial appendage that encloses ovule(s), then the gynoecium of B. rubra is carpellate. The basal ovule remains, however, cauline.

RÉSUMÉ

Développement floral de Basella rubra L.

La fleur de Basella rubra L. présente deux problèmes morphologiques: a) superposition des étamines et des tépales, b) placentation basale. a) Le premier problème traite de phyllotaxie. Si la définition classique de la fleur est considérée (une pousse monaxiale qui porte des phyllomes fertiles et stériles) les théories de phyllotaxie pourraient être utilisées pour expliquer la disposition des phyllomes sur l'axe floral. Une étude de la séquence d'initiation des étamines et des tépales révèle que les théories de phyllotaxie n'expliquent pas adéquatement le phénomène de la superposition. Un changement semble nécessaire dans la conception de théories de phyllotaxie et/ou dans l'interprétation de la fleur. b) Le deuxième problème se rapporte au carpelle. Ce dernier est traditionnellement défini comme étant un phyllome replié qui porte et renferme le/les ovule(s). Si cette définition est employée pour decrire le gynécée de B. rubra, il est acarpellaire parce que l'ovule prend forme directement de l'apex floral. Si le carpelle est redéfini comme étant un primordium gynécéen qui renferme le/les ovule(s), le gynécée de B. rubra est carpellaire. L'ovule basal demeure toutefois caulinaire.

TABLE OF CONTENTS

Page

INTRODUCTION

-General 1
-Superposition 2
-Basal placentation 10

MATERIAL AND METHODS 16

RESULTS

-General morphology 18
-Organogenesis
  1. Development of perianth and androecium 20
  2. Gynoecial development 21
-Development of vascularization
  1. Perianth and androecium 22
  2. Gynoecium ~~23~~

DISCUSSION

-General 25
-Superposition 26
-Basal placentation 32

LITERATURE CITED 37

FIGURES AND LEGENDS 57

APPENDIX I 67

Introduction- The plant kingdom is made up of an impressive number of diverse species. Variation in the form and structure within these species has interested many individuals over the centuries. This has resulted in the creation of ideas, concepts and theories that relate to and attempt to explain morphological variation. Angiosperm flowers are among the most widely investigated structures in plant morphology because of their numerous and most varied patterns. As more and more comparative developmental studies are made, problems arise when certain forms/structures cannot be explained according to existing theories. How should such cases be treated? Should they simply be considered as exceptions or should efforts be made to attempt to explain them? For example, how do we explain the flowers of Basella rubra L. (Basellaceae)? They present us with two controversial morphological phenomena. One involves phyllotaxis. The stamens instead of alternating with perianth members, as is the case for most flowers, are superposed to them. Another problem concerns the carpel concept: the gynoecium of this species has basal placentation.

The aim of this study is to document the development of the flower of B. rubra in order to determine: (i) whether existing phyllotactic theories adequately explain the phenomenon of superposition and, (ii) whether the carpel concept in its present form is applicable to the gynoecium of this flower. A secondary aim is to survey Angiosperm families to determine how widespread superposition and basal placentation are. For clarity, the phenomena of superposition and basal placentation will now be discussed separately in greater detail.

Superposition- Although known to taxonomists, superposition of androecial and perianth members seems to be neglected or has simply not been explored by most phyllotactic theorists (Rutishauser and Sattler, 1985). It is therefore important to bring such cases to light in order to understand what the underlying factors of such patterns might be. For this reason, the phenomenon of superposition of floral parts, more specifically the superposition of tepals and stamens in <u>B. rubra</u> will be dealt with in this study. We shall also be looking at cases of non-helical stamen initiation which closely resemble cases of superposition. The phenomenon of superposition is not entirely restricted to reproductive structures although it occurs more exceptionally and with less frequency than in flowers (Velenovsky, 1907; Troll, 1937; Guignard, 1984; Rutishauser and Sattler, 1985).

Superposition of androecial and perianth members is more common than was previously thought. It has been documented through developmental studies (Payer, 1857; Sattler, 1973; Posluszny and Sattler, 1973, 1974; Macdonald, 1974; Lyndon, 1978a,b, 1983; Milby, 1980; Pande and Singh, 1981; Rutishauser, 1981:34; Brett and Posluszny, 1982; Posluszny, 1983; Scribailo and Posluszny, 1984, 1985; Sundberg, 1982; Kirchoff, 1983;

Leins, 1983; Minter and Lord, 1983; Richards and Barrett, 1984; Rutishauser and Sattler, 1985; Posluszny et al, 1986; Posluszny and Gerath, in press). The species studied in the above mentioned reports come from a variety of Angiosperm families. To add to this diversity, the reader is referred to Appendix I which contains a list of all Angiosperm families identifying those in which superposition of perianth and androecial members is observed.

It would be misleading not to acknowledge other cases of non-helical stamen initiation in flowers which relate in some ways to cases of superposition but have different initiation sequences and/or involve more complex androecia. Such cases are also interesting in that they show the diversity of pattern and sequence of initiation of primordia. For example, superposition of stamens and perianth members as well as the centrifugal initiation of additional stamens was observed in Datisca cannabina (Leins and Bonnery-Brachtendorf, 1977). Similarly, Sattler and Singh, (1973, 1978) and Singh and Sattler, (1972, 1973, 1974, 1977) observed several cases of common petal-stamen initiation in the Alismatales. Some species of Loasaceae described by Leins and Winhard (1973) have flowers with a complex androecium that begin with the formation of ten complex organs (five episepalous and five epipetalous) that later differentiate into nectaries (three per episepalous organ), staminodes and many stamens (epipetalous organs). In the flowers of Asarum caudatum (Aristolochiaceae), six stamens are initiated in pairs on both sides of the inner perianth members. Later, additional stamens are centrifugally initiated in front of the inner and outer perianth members (Leins and Erbar, 1985). Certain tendencies were observed in selected species of Astrantia, Eryngium, Foeniculum, Hydrocotyle, Levisticum and Sanicula (Apiaceae). They are: overlaps in the sequence of initiation of calyx, corolla and androecium members such that stamen initiation parallels sepal initiation and initiation of common sepal-stamen primordia (Erbar and Leins, 1983). Erbar (1986) found superposition in flowers of Stewartia (Theaceae) between petals, stamen clusters and carpels. In selected species of Resedaceae some androecia originate from four primary primordia superposed to the four perianth members. Stamens later form centrifugally on these four primary primordia (Sobick, 1983). Endress, (1976, 1977) investigated flowers of Fothergilla (Hamamelidaceae) in which centrifugally developing stamen clusters arise superposed to sepals (corolla lacking). Rutishauser and Sattler (1985:445) state cases of androecial pattern formation such as: (i) the formation of common primordia which give rise to many stamens, (ii) stamen initiation in corners of the floral apex and subsequent lateral increase of stamen number until a ring is formed, (iii) superposition of consecutively initiated stamens and (iv) centrifugal stamen initiation.

Can these various androecial patterns, especially those dealing with cases of superposition of stamens and perianth members, be explained in terms of existing phyllotactic theories? If the classical view of the flower is accepted, that is that the flower is a modified monaxial shoot bearing fertile and sterile phyllomes, existing phyllotactic theories could be used in an attempt to explain cases such as superposition in flowers.

The literature on the subject of phyllotaxis is extensive and spans many centuries but has particularly flourished in the past fifty years. Recent reviews of phyllotactic theories (Rutishauser, 1981; Jean, 1984; Schwabe, 1984) stress this point but also show the diversity of perspectives/approaches to the problem. Schwabe (1984) categorizes the phyllotactic theories in three groups: (i) Largely descriptive systems, (ii) Mathematical systems not involving experimental approaches, (iii) Theories based largely on experimental approaches. Jean, (1984), a biomathematician, stresses more mathematical approaches. For the purpose of this investigation, the categories of phyllotactic theories used by Rutishauser (1981) will be considered. They are: (i) Field theories, (ii) Induction theories, (iii) Mechanical theories, (iv) Descriptive theories. Although these categories best reflect the main foundations of the theories, there is some overlap between them (see e.g. Rutishauser, 1981:110, table 12).

Field theories represent the majority of existing theories of phyllotaxis. According to these, existing growth centers (the apex and young primordia) diffuse a certain morphogen which is often thought to have an inhibitory effect. Thus, an inhibition field surrounding the young primordium forms and prevents the initiation of other primordia within that field. Since the inhibition diminishes with increasing distance from its origin, a new primordium can therefore only arise in an area of minimum inhibition. The nature of the morphogen (inhibitor or chemical mimicking such an effect) involved is still unresolved. The possible role of auxins has been hinted at (Wardlaw, 1955; Schwabe, 1971, 1984; Young, 1978). Over the years, the inhibition field theory has been modified, mathematically adapted and has also been used in computer simulations. Although concerned with the same basic concept, the field theories differ slightly in their assumptions and their power to explain various phyllotactic patterns. Spiral phyllotactic patterns are the main focus of field theories although some are concerned with other patterns such as whorled types of leaf arrangement. Among the most popular proponents of the inhibition field theory we find Richards (1948), Wardlaw (1952), Richards and Schwabe (1969), Schwabe (1971), Lyndon (1978a,b), some of them, such as Hellendoorn and Lindenmayer (1974), Schwabe and Clewer (1984), Veen and Lindenmayer (1977) using computer simulations, and other authors such as Thornley (1975a,b), Mitchison (1977) and Young (1978) using similar basic assumptions. Meinhardt (1982, 1984) and Harrison (1982) propose inductive as well as inhibitory effects of morphogens in their models. This list can be supplemented by consulting reviews by Rutishauser (1981:110 table 12) and Schwabe (1984:420 table 14.1).

Mechanical theories are the next most popular views. Instead of inhibition fields, physical aspects such as contact pressures and or competition for nutrients between primordia are thought to influence the positioning of new primordia. One of the first to propose a mechanical theory of phyllotaxis was Hofmeister (1868). The theory, known as Hofmeister´s rule, states that a new leaf is formed in the largest gap "grösste Lücke". More recently, Snow and Snow (1955, 1965) have revived Hofmeister´s ideas with their pioneering experimental approach by proposing a next available space theory. According to their numerous experiments, evidence supports the idea that a "minimum free area" of the apex is required for the positioning and initiation of a primordium. These sites become successively available in areas between existing leaves as growth proceeds. Williams and Brittain (1984) developed a geometric model simulating the requirements of the next available space theory. Along the same lines, Maksymowych and Erickson (1977) consider the initiation of primordia in these sites to be related to varying tensions on the surface of the meristem. A more mathematical mechanical theory of phyllotaxis is Adler´s contact pressure theory (1977). It is based on the assumption that the minimum geodesic distance between lattice points is maximized. Roberts´ chemical contact pressure model (1984), in which competition for nutrients is at the origin of the initiation of phyllotactic patterns, is proposed in conjunction with Adler´s contact pressure model.

A mechanical model which looks promising for the future, in light of recent experimental results, is Green's reinforcement field theory of phyllotaxis (Green, 1985, 1986 in press). Epidermal patterns of cellulose alignment in outer cell walls is thought to correlate with the initiation of phyllotactic patterns in vegetative and floral apices. The model is being tested further in more specific cases of floral development (personal communication).

Theories of induction are dominated by the French, the most famous theory being "la théorie des hélices foliaires multiples" proposed by Plantefol (1948) and later elaborated by Loiseau (1969). Two fundamental principles mark this theory: (i) the leaves are initiated along foliar helices which are most often multiple, (ii) at the end of each helix there is a leaf generating center. An organizer in the apex coordinates these centers. The helices, according to Plantefol can be traced up to the sepals in flowers and possibly to the petals in certain cases. Then there are theories of vascular determinism (see e.g. Bolle, 1963; Larson 1975, 1983), that is, procambial strand development dictates where a primordium forms. According to Larson (1983), more anatomical and developmental studies are necessary before this theory can gain wider acceptance.

Descriptive theories regroup older and more modern views including mathematical versions, most of which have already been referred to in the above categories. As can be seen by this brief account, many perspectives of the phenomenon of phyllotaxis exist.

Experimental studies of the pattern of primordial initiation in flowers and its relation to existing phyllotactic theories have been conducted but not as extensively as with vegetative structures. Plantefol (1948) and Loiseau (1969), as was stated above, trace their foliar helices all the way up to the calyx of some flowers. Uhl and Moore (1980) and Uhl and Drainsfield (1984) postulate a mechanical model for the initiation of stamens in major groups of palms. They believe that apical expansion and the stamen pattern "conform to pressures exserted by inflorescence bracts and perianth segments". Lyndon (1978a,b) uses Thornley's model of inhibitory fields in an attempt to explain the pattern of initiation of flower parts in _Silene_. Although phyllotactic concepts have been used to explain the pattern of primordial initiation in flowers, other authors maintain that there are differences which should be taken into account when applying phyllotactic principles to flowers (Leppik, 1956, 1961; Carr, 1984:453).

Along these lines, a detailed study of the spatio-temporal sequence of initiation of the perianth and the androecium of _Basella rubra_ L. was undertaken. The aim of this study was to document the phenomenon of superposition and to relate the pattern of initiation of flower parts to existing phyllotactic theories and/or alternate concepts.

Basal placentation- The extraordinary diversity in the form and structure of the gynoecium has been of interest to a great number of scientists over the centuries. As a result, the term carpel was coined to describe the gynoecia of Angiosperm flowers. Lorch (1963) conducted a unique and concise historical review of this term. He considers De Candolle (1813) principally and a few other authors from Germany and Great Britain as the first "discoverers of the idea of the carpel". It is also important to note that the term "carpel has been approached by a great number of botanical workers who have brought to bear on it widely different methodological and philosophical presuppositions" (Lorch, 1963). For these reasons, problems arose over the years with the growing use of this concept.

In its simplest and most basic form, the carpel is defined as a folded phyllome bearing and enclosing ovule(s), in the context of the classical definition of the flower which is a monaxial shoot bearing fertile and sterile phyllomes. According to Puri (1963, 1978), and the majority of botanists, the carpel is still the most "convenient instrument of description". This view is fully understandable because this particular concept has been applied to many gynoecial constructions successfully over centuries. Unfortunately, difficulties arise when the concept is applied to more complex types of gynoecial constructions. For example, in certain cases such as those involving some type of continuity between carpels, carpels and other floral organs and/or specific types of placentation such as free central or basal, the carpel cannot be clearly delimited in the context of the classical interpretation. Controversy therefore arises as to what is carpellary and what isn't, if such a determination can be made at all. Of particular interest to this study is the phenomenon of basal placentation and its applicability, if any, to the popular carpel concept. In this respect, the single basal ovule of Basella rubra L. presents us with a good case study.

Of special interest also are those studies dealing with the controversy over the position and initiation of ovules, that is, whether they are cauline in origin or borne on a phyllome, as the case would be with the classical interpretation of the carpel. The following list is by no means exhaustive. It simply points out those authors who have obtained results that support the existence of terminally initiated (cauline) placenta and/or ovule(s). Among studies of terminally initiated single basal ovules, that is, ovules which are not borne on phyllomes, we find works by Payer (1857) on several families, namely the Basellaceae, works by MacDonald and Sattler (1973) on Myrica gale (Myricaceae), Sattler (1973, 1974) also on M. gale and other families, MacDonald (1974) on Laportea canadensis (Urticaceae), Galle (1977) on selected species of Polygonaceae, Tucker (1980, 1982) on selected species of Piperaceae, Sattler and Perlin (1982) on selected species of Nyctaginaceae. These studies represent good examples of basal ovules. Basal or terminal ovules have also been extensively studied in grasses in studies by Mehlenbacher (1970) on Oryzopsis hendersoni and Maze et al (1971) on Oryzopsis miliacea, to state a few. A beautiful S.E.M photomicrograph depicting a similar condition in Zea mays was presented in a paper by Cheng et al (1983:456, fig.19). Ovules of more complex gynoecia, still believed to arise from the floral apex in the axil of phyllomes as opposed to being borne on them are featured in works by Bessey (1898) on the Ranunculaceae, Alismaceae and Rosaceae, Dengler (1972) on Calycanthus occidentalis (Calycanthaceae), Van Heel (1978) on the Malvaceae, Pauzé and Sattler (1979) on Ochna atropurpurea, Richard and Tucker (1979) on Illicium floridanum (Illiciaceae), Gemmeke (1982) on selected species of Mimosaceae and Uhl and Dransfield (1984) on selected species of palms. Other studies involving the development of a central placenta directly from the floral apex are documented and presented by Moeliono (1970) on selected species of Caryophyllaceae, Primulaceae as well as other families, and Aymard (1970) on Cyclamen persicum (Primulaceae). This list can be supplemented by consulting Appendix I for an approximation of the frequency of Angiosperm families which have been described as having basal placentation. The above list reflects the interpretations of the various authors and serves to point out cases which are difficult to explain in the framework of the classical concept of the carpel thereby showing the limits of applicability of such a model. As a result, some authors have evolved alternative models of the origin of the flower (Grégoire, 1938; Croizat, 1962; Lam, 1962; Melville, 1962; Meeuse, 1963). These will be discussed further in the conclusion of this study.

Although some authors believe that the classical concept is inadequate for certain types of gynoecial constructions like those enumerated above, others still maintain that all placentae are parts of carpels and consequently that there are no such things as cauline ovules in Angiosperms (Wilson and Just, 1939; Eckardt, 1955; Parkin, 1955; Eames, 1961; Puri, 1963; 1978; Guédès, 1979). Eames (1961) even goes as far as saying that "when evidence from all fields are considered, none of the twentieth century concepts of the nature of the carpel can displace the classical view that the carpel is a fertile lateral appendage". The main criterion utilized by this and other authors (see e.g. Eckardt, 1954; Parkin, 1955) is the vascular anatomy of the flower, believed to be more conservative through evolution than external morphology. Therefore, according to them, the patterns of vascular connections (i.e. curved strands, residual strands) reveal the 'true' lateral position of carpels and their appendicular ovule(s). In cases such as these, the term basal placentation is used in a more descriptive sense, especially if it is considered as derived from a more primitive type of placentation as a result of reduction (Eames, 1961; Puri, 1963, 1978).

Another way in which the classical interpretation of the carpel is extended to accommodate cases that are more difficult to explain such as cauline ovules is to invoke the concept of congenital fusion. In these particular cases the basal part of the carpel, i.e. the cross zone (Querzone) is believed to be congenitally fused with the floral apex. The ovule(s) which appear to be inserted terminally are actually initiated on this cross zone of the carpel. The gynoecium is therefore compared to a terminal peltate leaf. By postulating this type of construction the carpel concept still stands, but not without some opposition (see e.g. Sattler and Perlin, 1982).

From his observations on the diversity of floral constructions, Lam (1962) concluded that two concepts are necessary to explain such diversity among Angiosperms: phyllospory and stachyospory. In phyllosporous flowers, the sporangia are borne on phyllomes. This particular concept agrees with the classical concept of the flower. Stachyospory, on the other hand, involves a state in which sporangia (ovules) are borne on the floral axis as in Basella. Two types of Angiosperm flowers are therefore believed to have evolved. Although it seems to explain the existence of stachyosporous and phyllosporous flowers, the difficulty with this theory, according to Sattler (1965), is "the existence of intermediates between the two types, which make it hard to accept any fundamental difference between the basic types".

In light of the above interpretations of the carpel, that is, whether ovules are cauline, carpellary, or both, a study of the development of the gynoecium of Basella rubra L. (Basellaceae) was undertaken. The aim of this study is to determine whether the single basal ovule of this species is initiated terminally (axial) or if it is carpellary. A secondary aim was to conduct a survey of Angiosperms to determine the approximate frequency of families, in addition to the Basellaceae, with basal placentation.

MATERIAL AND METHODS- Developing inflorescences of <u>Basella rubra</u> L. were periodically collected from October 1984 to December 1985 from the McGill University greenhouse. 350 flower buds of different developmental stages and approximately 100 mature flowers were examined. The plants were grown under normal greenhouse conditions. Material was identified according to the key in the Flora of Java by Backer (1963) and Flora Malesiana by Van Steenis (1958) at the genus level and in the Manual of Cultivated Plants by Bailey (1949) and in an article by Fathima et al. (1971) at the species level. A voucher specimen has been deposited at the McGill University herbarium at the MacDonald College campus in Ste. Anne de Bellevue, Québec.

Epi-illumination technique- Specimens were fixed in formalin-acetic acid-alcohol (FAA) from 12 hours to an indefinite period of time. Following fixation, material was dehydrated through a gradated ethanol series, stained in 5% (w/v) alcoholic acid fuchsin, dissected in 95% alcohol and photographed with an epi-illumination microscope following the technique of Posluszny et al. (1980). Stain intensity was varied through differing staining times to highlight certain developmental stages of individual flower buds.

Light microscopy- Flower buds that were fixed in FAA were dehydrated in a gradated tertiary butyl alcohol series and embedded in paraffin (tissue prep. m.p 61°C). Serial sections approximately 7µm thick were stained in Delafield's hematoxylin or in Astrablue with a Fuchsin and Picric acid counterstain.

Flower buds that were used for thin sectioning were fixed in either 3% glutaraldehyde in 0.1M sodium phosphate buffer pH 7.2 , 3% glutaraldehyde in 0.03M PIPES buffer pH 7.0, or 2% glutaraldehyde in 0.1M cacodylate buffer pH 7.2. Material fixed in cacodylate buffer and sodium phosphate buffer both gave excellent fixation in comparison to material fixed in PIPES buffer but the sodium phosphate buffer was preferred mostly for safety in preparation and handling. All glutaraldehyde fixed material was first washed in several changes of buffer and either postfixed in buffered 1% osmium tetroxide and dehydrated through a gradated ethanol series or stained in 5% acid fuchsin at a certain point in the dehydration series. Either method facilitated orientation during embedding in SPURR plastic (Spurr 1969) or LR white resin (data sheet available from J.B.EM services incorporated). Sections of 2µm were cut on a Sorval Porter Blume MT-2 microtome, using glass knives. They were stained with 0.1% methylene blue in 1% borax, dried, mounted with coverslips and photographed on a Zeiss photomicroscope.

Clearing-Some FAA fixed flower buds and inflorescences were cleared according to the technique of Fuchs (1963) to reveal vasculature.

RESULTS- General morphology- Basella rubra L., also called Malabar spinach, is a small perennial herb, native of tropical Africa and Asia (Van Steenis, 1958), with a purplish red twining stem bearing spirally arranged leaves. Small spike-like inflorescences are situated in the axils of leaves. Each inflorescence is composed of several flowers that mature acropetally (Fig.2). Although most flowers are cleistogamous, at least under greenhouse conditions, some open slightly at maturity (Fig.3). All the perianth members of the flowers are purplish red in color at the tip and white basally. Each flower is subtended by a bract and, at its base bears two lateral bracteoles, one abaxial and one adaxial involucral bract. The latter have also been interpreted as two sepals (Bailey, 1949; Backer, 1963; Bogle, 1969; Cronquist, 1981; Sharma, 1961). There are five tepals superposed to five tetrasporangiate stamens and a tristigmate gynoecium, containing a single basal ovule (Fig.1). Of the approximately 100 mature flowers randomly selected from the same or different plants, no major difference in aestivation was observed. The subtending bract and the lateral bracteoles are vestigial when the flower is at or near maturity (Fig.3). Overlapping of these structures was consequently not observed. The adaxial involucral bract overlaps with the abaxial one at its tip. Both are continuous at the base and appear tepaloid. The two lateral tepals toward the abaxial side cover the remaining floral parts almost completely. The margins of the abaxial tepal are inside the latter. The two tepals toward the adaxial side overlap each other on different sides with equal frequency (Fig.1). The five tepals are continuous at their base at a slightly higher level than the adaxial and abaxial involucral bracts. At their base, the five stamens and the tepals are inserted on a continuous fleshy tube which is free from and surrounds the gynoecium. Therefore, the stamens appear epitepalous.

Organogenesis- The subtending bract is the first structure to be initiated on the inflorescence axis. In its axil, the floral apex develops. Histologically, it has a two-layered tunica and corpus (Fig.10). As the floral apex grows in size and becomes rounder, a bracteole is initiated laterally on both sides (Fig.4). These two structures appear to be initiated simultaneously. During the early stages of development, they cover the floral apex, although only partially (Fig.4). Next, the adaxial and abaxial involucral bracts are also simultaneously initiated in a plane perpendicular to the bracteoles (Fig.4,5). The involucral bract primordia take up a wider portion of the floral apex upon their initiation than the bracteoles and continue to grow to cover the remaining floral parts at maturity unlike the bracteoles which are vestigial in the mature flower.

1.Development of the Perianth and Androecium- The first tepals to arise are the two lateral ones toward the abaxial side. They are initiated simultaneously as dorsiventral primordia (Fig.5-8). Next, two tepals toward the adaxial side and the abaxial tepal appear. Their sequence of initiation appears simultaneous, although in some cases the abaxial tepal may arise slightly later (Fig.7-9). When all the tepals have been initiated, stamen primordia emerge from the floral apex, each one superposed to a tepal primordium (Fig.9,14,15). The first two tepals to be initiated grow to a considerable size compared to the other tepals before their superposed stamens (those toward the abaxial side) are initiated. The time interval between the initiation of other tepals and their superposed stamens seems to be shorter as evidenced by the smaller size of those tepals upon the initiation of stamens. The sequence of initiation of stamens mirrors that of the tepals (Fig.8,9). Long files of cells were seen to extend from the floral apex where a stamen will be initiated to the surface of the superposed tepal primordium (Fig.6). Each stamen primordium is dorsiventral (Fig.9,14-16). There is, however, some variation in the shape of this primordium during early stages of initiation. The stamen primordia toward the abaxial side appear laterally more elongate than the adaxial ones (Fig.15,16). Both the tepal and the stamen primordia are initiated in the same manner, each arising through periclinal divisions in the second and underlying cell layer and concomitant anticlinal divisions in the outermost cell layer and below (Fig.10,11). Although the tepals are initiated before the stamens, their growth lags behind that of the latter (Fig. 11-13,16,17), until shortly after thecae form (Fig. 18,19).

2.Gynoecial Development- When all the tepals and stamens have been initiated and have grown to a certain size (Fig.20), the slightly convex floral apex gradually assumes a triangular shape as a result of the inception of three gynoecial primordia (Fig.20,21). These primordia arise from anticlinal and periclinal divisions in the second cell layer and underlying cells and concomitant anticlinal divisions in the outermost layer and below (Fig.31). As the three appendages grow, the remaining floral apex becomes more rounded and dome shaped, thus gradually transforming into a single ovule (Fig.22-25). The transformation from floral apex into ovule is so gradual that it is impossible to pinpoint exactly when the floral apex becomes the ovule. As the ovule primordium develops, the meristematic appearance of cells such as dense cytoplasm, numerous small vacuoles and actively dividing nuclei shows no change, at least at the light microscope level (Fig.31-34). A two-layered tunica, apparent in the earlier stages of floral development is maintained until the primordium has become distinctly dome shaped (Fig.33). In the following stages, periclinal divisions occur in the second layer. The inner integument is initiated before the outer one through anticlinal and periclinal divisions in the outer cell layer and in the underlying layer (Fig.27,35). The gynoecial primordia form the three stylar branches that are continuous at the base at maturity. The ovary wall that encloses the ovule results from interprimordial growth at the base of the gynoecial primordia (Fig.26,29).

When the two integuments have completely developed and the ovule has become ortho-amphitropous (Fig.30), the gynoecium appears trilocular at the base. The locules are approximately .17-.2 mm deep (approx. 15% of total ovary height) as was determined by serial cross-sections. The ovule is not enclosed in any of the three locules, but rather lies on top of them (Fig.28). However, the micropyle terminates in one of the locules (Fig.36,37).

Development of vascularization- 1.Perianth and Adroecium- The differentiation of the procambium in the flower is acropetal. One strand differentiates after the initiation of each primordium. The vascular supply to the flower is initiated in the form of two strands to the adaxial and abaxial involucral bracts. As the first two tepals toward the abaxial side are initiated, the abaxial involucral bract strand branches on both sides. The supply to the next three tepals to be initiated (the abaxial one and two others toward the adaxial side) originates much in the same manner. The abaxial tepal branches from the abaxial involucral bract strand and the supply to the two tepals toward the adaxial side is derived from the branching of the adaxial involucral bract strand. The vascular supply to each of the five superposed stamens originates from branches of the tepal strands. In the mature or nearly mature flowers these vascular connections can be observed in relation to each other. Two main areas of differentiating vascular tissue each radiate into three main strands toward the adaxial and abaxial sides (Fig.42a-b). The abaxial strand supplies the abaxial involucral bract, the abaxial tepal and superposed stamen. The other two lateral strands toward the abaxial side each supply a tepal and its superposed stamen (Fig.42c-e). The adaxial strand supplies the adaxial involucral bract. The other two laterally adaxial strands each supply a tepal and its superposed stamen (Fig.42c-g). In some flowers, the lateral strands toward the adaxial side also supply secondary strands to the adaxial involucral bract (Fig.42c,arrow). These additional connections vary from flower to flower as was concluded from serial cross-sections and clearings of nearly mature and mature flowers.

2.Gynoecium- The development of the procambial supply to the gynoecium is the result of branches of the tepal-stamen strands. These strands converge in the center of the axis, thus forming a nearly circular ring of provascular tissue. From this, three gynoecial strands branch, each supplying one of the three developing gynoecial appendages. These vascular connections can be seen in their nearly mature state in Fig. 38-40, 42c-e. In more mature stages, six strands are seen in the gynoecial wall: three major strands and three additional ones (Fig.36). Branch strands from these six merge centrally to form one strand to the single central ovule (Fig.39,41).

Discussion- In the specimens studied, all flowers had five tepals and five stamens. No deviation from superposition was observed. The majority of family and/or species descriptions (Van Steenis, 1958; Sharma, 1961; Backer, 1963; Bogle, 1969; Fathima et al, 1971) agreed with the observations made for B. rubra concerning the arrangement and number of floral parts. Other authors, however, fail to mention certain flower parts that were observed in this study and in the majority of other descriptions. For example, in the family descriptions by Bailey (1949), Melchior (1964), Willis (1966) and Cronquist (1981), no mention is made that each flower is subtended by a bract followed by two or four bracteoles (in this case two bracteoles and two involucral bracts). Additionally, a discrepancy in the naming of perianth members was noted. Involucral bracts, a term used in this study, were identified as sepals and bracteoles. Some authors qualify the flower pattern of B. rubra as tricyclic (Payer, 1857; Eichler, 1878; Melchior, 1964).

Payer's (1857) observations on the floral development of B. rubra were similar to those made in this study. Some differences were noted however. According to Payer, the two involucral bracts are not initiated simultaneously but rather sequentially. In the material used for this study, however, the involucral bracts appear to be initiated simultaneously. A difference in the shape of the two involucral bracts occurs early in development (see Fig.4,9) which might explain this discrepancy. Another more important difference in Payer's description is the presence of a sixth stamen primordium that is initiated superposed to the adaxial involucral bract and later aborts. No such evidence of a sixth stamen primordium was found in any of the flowers examined in this study. Eichler (1878) in his short description of the Basellaceae discusses Payer's results. He does not support Payer's idea of an aborting sixth stamen, contrary to what was reported in Bogle (1969). The presence of a sixth stamen is not mentioned in any other relevant literature known to the author.

Superposition- Results of this study support the statement that stamens and tepals in flowers of B. rubra are superposed to one another. The actual sequence of initiation of stamens and tepals is: two tepals toward the abaxial side, three other tepals (two toward the adaxial side and one abaxial), two stamens toward the adaxial side and three other stamens (two toward the adaxial side and one abaxial). Thus, the spatial and temporal pattern of initiation of stamens and tepals can be compared to a 2+3 arrangement, although the abaxial tepal or stamen seems to lag in its initiation. Such changes in patterns, however, are not unique to this species. Gomez-Campo (1974), Heimans (1978) and Zagorska-Marek (1985) report cases in which phyllotactic patterns changed within one individual. According to those authors, the underlying factors of the transitions remain obscure although apex size/shape seemed to be involved. The spatio-temporal pattern of tepal-stamen initiation in B. rubra leading to superposition of those structures does not seem to fit the general phyllotactic patterns such as spiral and whorled arrangements, outlined in the existing phyllotactic theories.

Superposition is a phyllotactic problem that seems to have been neglected by existing phyllotactic theories. This phenomenon is not restricted to the Basellaceae but is more frequent than we think, at least in flowers. Appendix I conveys an idea of the number of Angiosperm families exhibiting superposition of perianth and androecial members. Since not all of the Angiosperm families reported in Appendix I were studied developmentally, the results only approximate the number of cases of superposition.

Some recent publications dealing with phyllotaxis and its application to flowers expose the problem of superposition and attempt to furnish an explanation of the phenomenon. Their results could possibly be applied to the arrangement of tepals and stamens in B. rubra. For example, Young (1978) considers that his diffusion model can explain various "subpatterns of axillary organs which are superimposed on a primary phyllotactic pattern". He also believes that his model could eventually be applied to floral morphogenesis. Thornley (1975a) on the other hand states that his own model involving the diffusion of an inhibitor fails for "whorls where leaves in adjacent whorls lie vertically above one another". He maintains that a further modification of the model would be necessary in which "repulsive" properties would be made "attractive" (Thornley, 1975a:505). With the accumulation of more experimental data, Thornley also believes that his model could be applied to flowers and the arrangement of their parts.

Also of relevance to the problem of superposition is a study of the initiation of flower primordia in *Silene* and their relationship to phyllotaxis (Lyndon, 1978a,b). In this particular case, stamens arise in the axil of the sepals and petals. Factors which resemble those governing the initiation of axillary buds and others which resemble factors determining leaf initiation are postulated in this particular model. Lyndon therefore concludes that the early development of the flower of *Silene* resembles "a condensed leafy shoot with precocious axillary buds". In this context, *B. rubra* stamens could also be considered as axillary structures because of their superposition to tepals.

Superposition of stamens and tepals in *B. rubra* is also reflected in the pattern of vascular connections. The supply to the stamen branches off from the strand supplying the tepal in all cases, demonstrating the close spatial relationship between tepals and stamens. The pattern of vascular strands and their branching in mature flowers of *B. rubra* described by Sharma (1961) seems to agree with what was observed in this study. Since the development of the vascular supply to the flower was not described by Sharma (1961) or Saunders (1939a), comparison of results is difficult. Although there might be a close relationship between the arrangement of primordia and the vascular differentiation pattern in certain cases (see e.g. Girolami, 1953; Larson, 1975; Kirchoff, 1984), no evidence was found in B. rubra to favor the view that procambial strand development precedes primordium formation. The relation between acropetally developing procambial strands and primordium inception at the apex, if any, is still a source of controversy and remains unresolved (Larson, 1975).

An important point to consider in light of the problem of superposition is the interpretation of stamens. According to the classical view, stamens are fertile phyllomes. As in most cases, there is some opposition to this view (Melville, 1963; Lyndon, 1978a,b; Meeuse, 1980, unpublished, to name a few). As a result of the above studies (Thornley, 1975a; Lyndon, 1978a,b; Young, 1978), it would seem, in the case of B. rubra and possibly also in other cases mentioned in this study (see Introduction), that stamens or stamen clusters could best be interpreted as axillary, branch-like structures invoking the branchlet hypothesis. This in turn would coincide with the "fertile leaf" model of the shoot where stamens could arise "in the axil or as part of a tepal primordium" (Rutishauser and Sattler 1985). The main proponents of such a model (Arber, 1950; Croizat, 1962; Melville, 1963; Meeuse, 1980, unpublished) developed schemes which are mostly phylogenetic.

Of relevance to the explanation of superposition, more specifically stamens as axillary structures, is Meeuse's anthocorm theory (1980, unpublished). He believes that flowers are pluriaxial. Therefore, they cannot be compared to a leaf bearing axis, that is, reproductive organs cannot be homologized with leaves. The basic structure of the flower is the gonoclad, a bracteated cladic organ bearing sporogenous appendages. Evolutionary specializations are believed to have produced several alternative structures leading to the different patterns observed today.

Another alternative interpretation of the classical concept of the flower, which could explain stamens as axillary structures is Melville's gonophyll theory (1963). The basic unit of the flower in this case is the gonophyll, a leaf bearing one or more fertile branches. The evolution of such a structure, through different processes, as evidenced by many derived forms often at the source of controversy, is outlined in Melville (1963). Other proponents of the fertile leaf model, an alternative view to the classical concept, such as Arber (1950), Croizat (1962), Dickinson (1978) and Cusset (1982) are among the many authors who's models could explain stamens in terms of axillary structures. The majority of those authors, however, accept more than one model in that their views are not totally restricted to one concept.

The phenomenon of superposition outlined in the Introduction is evidence that not all flowers can be easily described in the framework of the classical concept of the flower and that consequently the interpretation of stamens as microsporophylls is questionable (see e.g. Nozeran, 1955; Heinsbroek and Van Heel, 1969). The opposite is also true in that numerous flower patterns can be described according to the popular classical concept (see e.g. Carlquist, 1969; Endress, 1983). With which structures should stamens therefore be compared, leaves or shoots? Or is this a valid question? According to Rutishauser and Sattler (1985), the "units stem and leaf are probably much more arbitrary categories than often assumed".

Evidence from this study tends to support the interpretation of stamens in B. rubra as axillary structures. The few phyllotactic theories dealing with superposition, interpret superposed structures in terms of axillary structures. Unfortunately, no definite model has been advanced to explain superposition of certain flower parts. However, the classical concept of the flower should not be disregarded. It does have some predictive power in other cases. It is obvious that more studies are needed to gain a better understanding of the phenomenon of phyllotaxis especially in its application to flowers, hence the necessity for more comparative and experimental developmental studies.

Basal placentation- The results of this study support the view that the single basal ovule in Basella rubra L. is cauline. It is a direct transformation of the floral apex and therefore terminal, i.e. it is not borne on any of the three carpel primordia. As a result of this interpretation, the gynoecium of B. rubra is acarpellate, if described in terms of the classical concept of the carpel. However, if the carpel is redefined as a phyllome enclosing, not necessarily bearing, ovule(s), the gynoecium of B. rubra can still be considered carpellate.

Attempts were made to interpret the gynoecium of Basella in terms of the classical carpel concept (Eckardt, 1955; Sharma, 1961, 1968). The evidence for such an interpretation was: (i) the presence of septa for a short distance at the base of the gynoecium, (ii) the vascular supply of the gynoecium, (iii) the position of the ovule toward the adaxial side (toward the adaxial gynoecial primordium). The presence of septa for a short distance at the base of the gynoecium is interpreted by Sharma (1961, 1968) and Eckardt (1955) as the result of an extreme reduction in an axile type of placentation i.e. ovules were originally carpellary. This condition has also been observed in other members of the Basellaceae, namely Boussingaulthia gracilis and Basella alba (Eckardt, 1955; Moeliono, 1970). Additionally, Sharma (1961) believes that the vascular supply to the gynoecium of B. rubra might be further evidence of a reduced axile placentation. He states that the anastomosing of "small vascular elements" forming the central supply to the ovule "clearly" shows that "some axial tissue" persists but that "the nature of this bundle further up (whether it is purely ovular, or if it incorporates some ventral bundles as well) is not clear". He also maintains that it is possible that more than one "ventral" strand can supply a single basal ovule. He concludes that the placentation in the gynoecium of Basella "clearly shows the ovule to be a lateral organ". Eckardt (1955) maintains that the position of the ovule in the gynoecium of B. rubra is further evidence of its carpellary nature. According to him, the ovule is closer to the adaxial "carpel" primordium and, as a consequence, is possibly associated with it. Eckardt's (1955) results are substantiated by similar studies on other members of the Basellaceae such as Boussingaulthia gracilis and Basella alba.

Is the evidence presented by Eckardt and Sharma sufficient or adequate enough to explain the gynoecium of B. rubra in terms of the classical concept of the carpel? In view of the above and keeping in mind the primary aim of this study, which is to determine whether the basal ovule of Basella is cauline or carpellary, the development of the gynoecium was studied from the point of view of developmental morphology. In the material used for this study, septa arise at the base of the gynoecium of B. rubra but only secondarily, that is, well after the ovule is initiated on the floral apex in its central position, in relation to the three 'carpel' primordia. In this case it is difficult to accept that the single basal ovule of Basella is borne on a reduced axile placenta. Even if the final product is an ovule inserted on a basally trilocular gynoecium, evidence from this study still supports the view that ovule initiation precedes and is independent from the formation of septa. In addition, the position of the ovule is not the same at all as in axile placentation. Moeliono (1970) arrived at a similar conclusion in his interpretation of septa in the Basellaceae.

In his interpretation of basal placentation in B. rubra, Sharma (1961) also uses the vascular supply of the gynoecium as a case for vascular conservatism by stating that the possible ventral nature of "bundles", even if there are more than one supplying the ovule, could be an indication of the carpellary nature of the ovule. It is not as clear or definite to the author whether the vascular pattern observed in the gynoecium of B. rubra is the remnant of an axile type of placentation or simply the result of normal processes of development. According to Carlquist (1969), there is no reason to believe "the vascular system lags behind external form to any appreciable degree (see also Schmid, 1972).

The position of the ovule closer to the adaxial "carpel" in Basella (Eckardt, 1955) was not apparent during the early developmental stages of the gynoecium. The orientation of the ovule toward the adaxial "carpel" in later stages is believed to be the result of the curving and subsequent growth of the ovule, its micropylar end terminating in the deepest of the three locules (the one toward the adaxial side). No histological or developmental evidence was found to link the ovule preferentially to one of the three ´carpels´.

The author´s findings that the ovule of B. rubra is cauline is a conclusion of developmental morphology. The existence of cauline ovules and placentae has also been demonstrated in several other species (see e.g. Introduction, Sattler, 1974; Philipson, 1975). A survey of Angiosperm families also reveals that basal placentation is not restricted to the Basellaceae and other closely related families. This type of placentation is found in approximately 10% of Angiosperm families (see Appendix I).

With regard to the evolution and phylogeny of the cauline ovule, there are two possibilities: (i) the cauline ovule is a primitive condition, (ii) the cauline ovule is a derived condition. This issue, according to Philipson (1975) is still unresolved. In addition, other authors (see e.g. Maze et al, 1971; MacDonald and Sattler, 1973) do not dismiss the possibility of a polyphyletic evolution of Angiosperms. In view of the diversity and controversy concerning the above interpretations, a more descriptive approach to gynoecial morphology has been proposed by Sattler (1974). The term gynoecial appendage is used for the mature structure that develops from a gynoecial primordium. This primordium gives rise to part of or the whole gynoecium with the exception of placentae and/or ovules. Placentation and gynoecial appendage are therefore considered separately. The different gynoecial constructions are related to one another "as a result of basic processes that operate on gynoecial primordia, placental primordia, ovular primordia and the primordia of surrounding tissues and organs" (Sattler, 1974). These processes are: 1. spatial shifting, 2. temporal shifting, 3. zonal growth, 4. fusion, 5. reduction, 6. amplification, 7. modification, 8. transference of function. This approach has the advantage of not being dependent on theories of evolution of the flower. In the particular case of the gynoecium of B. rubra, one could for example explain the basal ovule in the context of the classical concept as the result of spatial shifting, that is, a change in the position of ovule initiation from the phyllome or gynoecial appendage to the floral axis. According to Sattler (1974), the opposite could also be true, that is, ovule inception could shift from a position on the axis to a position on the gynoecial appendage, invoking other models of evolution of the flower. Proponents of such models interpret the fertile part of the gynoecium as cauline and the sterile part as one or more bracts (Croizat, 1962; Meeuse, 1963), stegophylls (Lam, 1962), tegophylls (Melville, 1962) or phyllomes (Moeliono, 1970).

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Fig.1. Diagram of a mature flower showing subtending bract, 2 lateral bracteoles, 2 involucral bracts (one adaxial and one abaxial), 5 tepals superposed to 5 tetrasporangiate stamens, and a tristigmate gynoecium enclosing a single bitegmic basal ovule. Dot represents inflorescence axis.

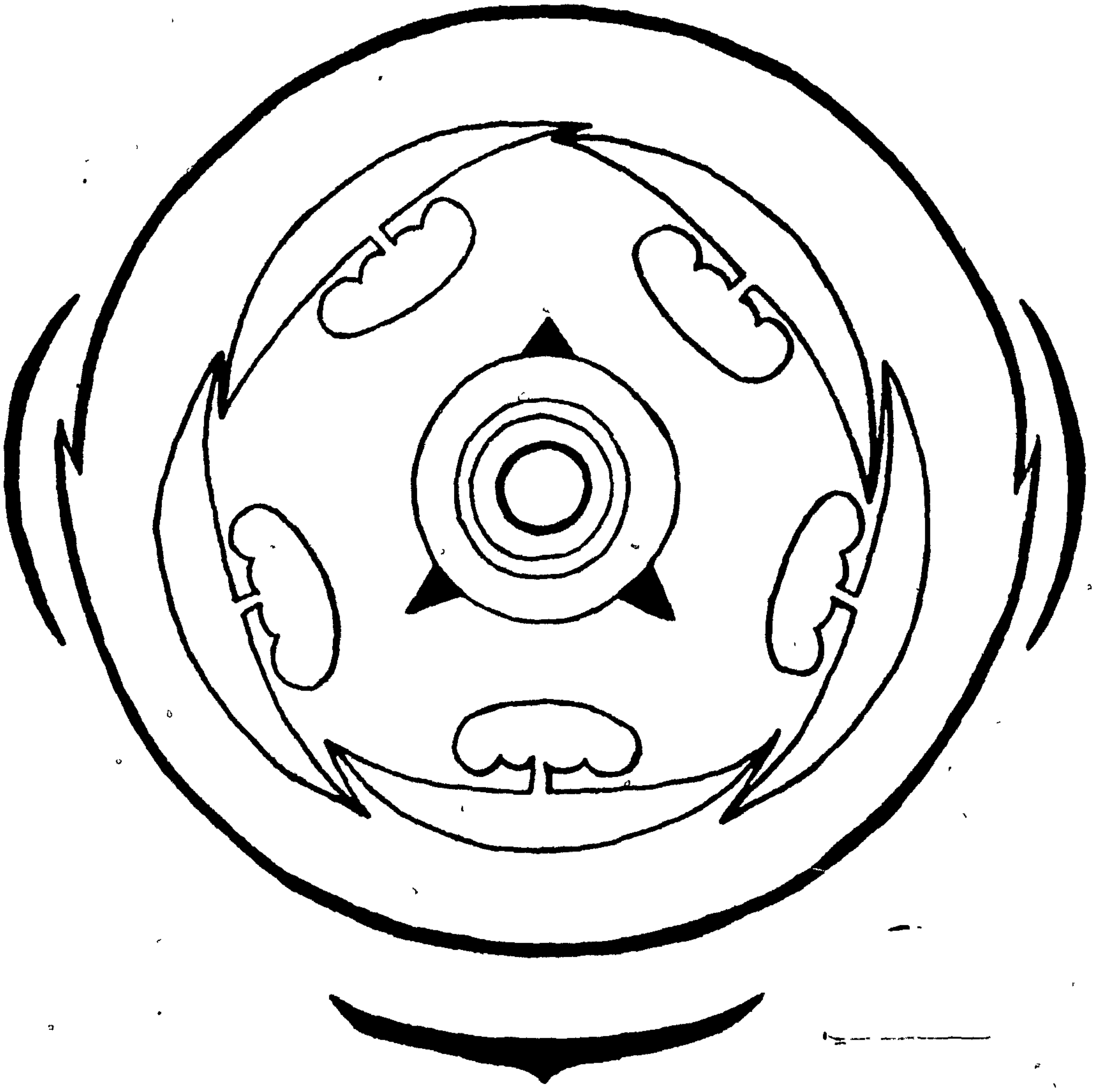

Fig.2-5. 2. Inflorescence subtended by a leaf, X1.4. 3. Close-up of lower flowers in Fig.2 showing one slightly opened flower where the two involucral bracts (arrowheads), stamens and tepals are visible, X5.3. Fig.4-5. Epi-illumination photographs of developing flower buds. 4. Side view of inflorescence tip showing flower buds at different developmental stages: a young bud centrally with two bracteoles (b) and a subtending bract (rB), which has been removed, a slightly older bud to the left showing the involucral bracts (Biv), a still older stage lowermost showing bracteoles (b), involucral bracts (Biv), and first formed tepals (P) toward the abaxial side, X126. 5. A slightly tilted older flower bud showing bracteoles (b), involucral bracts (Biv), the first two tepals (P) and the initiation of the 3rd, 4th and 5th tepals (arrowheads), X144.

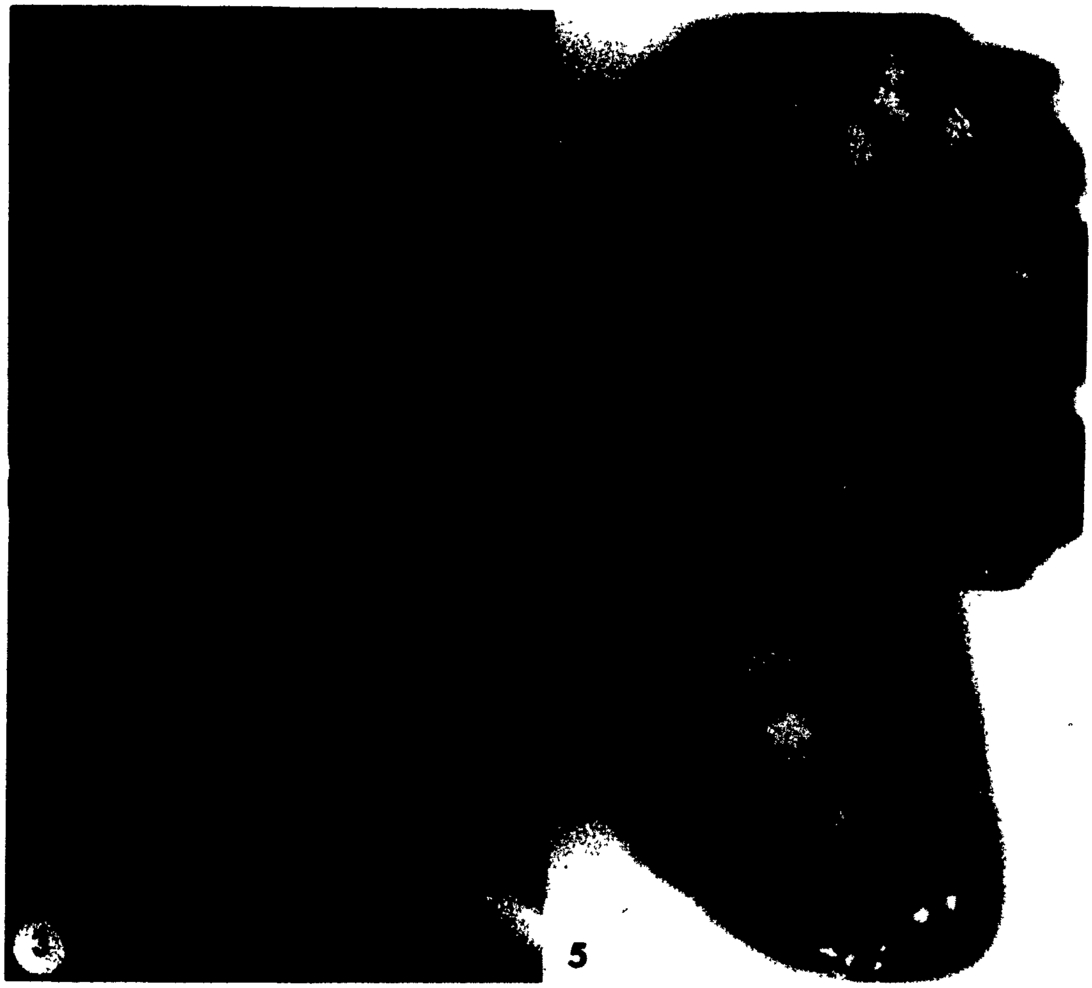

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Fig.6-9. Épi-illumination photographs of sequential initiation of tepals and stamens. 6. Side view of first formed tepals (P) toward the abaxial side . Cell files extend from the tepal primordia upward where stamens will be initiated, X162. 7. Side view of an older flower bud where the 3rd, 4th and 5th tepals (P) have been initiated and the first two stamens toward the abaxial side are just forming (arrowheads), X162. 8. Top view of a stage similar to that of Fig.7 showing the first two tepals (P). The abaxial tepal primordium is not apparent in this case, X162. 9. Top view showing all five tepals (P), the two first formed stamens (A) superposed to the tepals and areas where the last three stamens will be initiated (arrowheads), X162. Dot indicates inflorescence axis.

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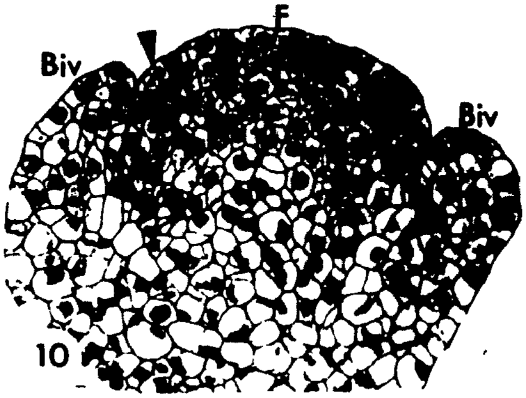
Fig.10-13. Photomicrographs of median longitudinal sections of different developmental stages of flower buds in the adaxial-abaxial plane featuring the development of the abaxial tepal and stamen and tunica-corpus organization of the floral apex (F). Biv=involucral bract. 10. Periclinal cell divisions below the outermost cell layer (arrowhead) indicate where the abaxial tepal is initiated, X300. 11. Early development of tepal (P) and superposed stamen (A). Periclinal cell divisions are apparent directly below the outermost cell layer and even below the second layer, X300. 12. Older stage showing size difference between the developing tepal (P) and stamen (A), X256. 13. Still more advanced stage before the formation of the gynoecium, X224.



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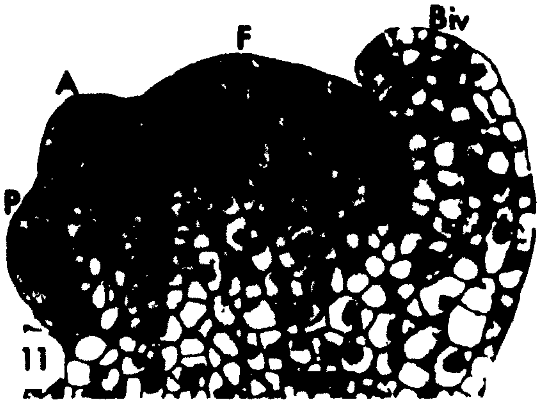

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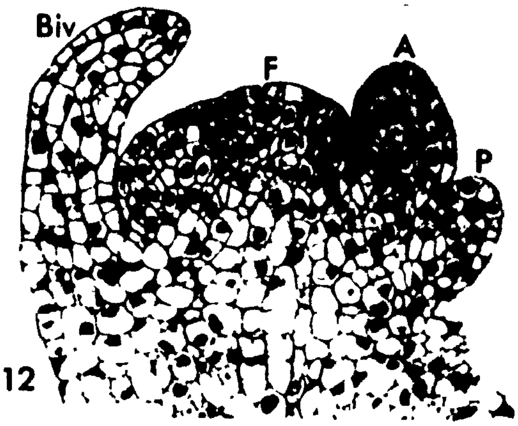

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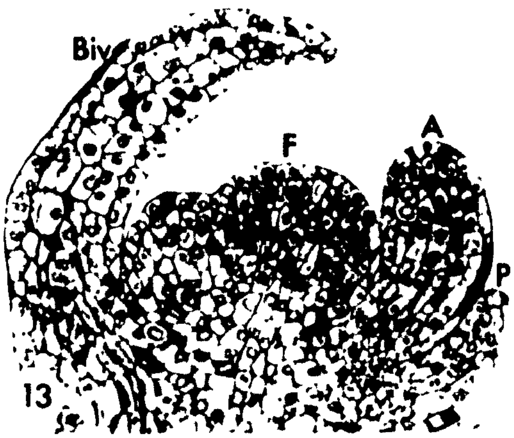

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Fig.14-19. Epi-illumination photographs of flower buds. 14. Top view showing the initiation of the stamens opposite the third, fourth and fifth tepals (P). The abaxial tepal is covered by the involucral bract (Biv), X144. 15. Slightly older stage than that of Fig.14. Note greater continuity between the stamen primordia toward the abaxial side (arrowheads), X144. 16. Top view of an older developmental stage. All five stamens (A) are superposed to the tepals (P), X144. 17. Side view of a flower bud during theca (T) formation showing closely associated superposed stamens (A) and tepals (P), X144. 18. Top view of an older bud. Stamens have been removed (rA) to show their relationship to the tepals (P), X84. 19. Side view of a stage similar to that of Fig.18 showing that some growth (arrowhead) has occurred below the insertion of the stamen (A) and tepal (P), X84.

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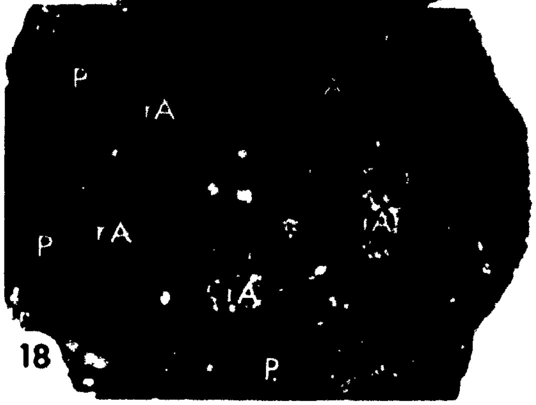

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Fig.20-27. Epi-illumination photographs showing the development of the gynoecium. 20. Top view of a flower bud showing the inception of the three gynoecial appendages (arrowheads). A=stamen, P=tepal, X144. 21. Side view of floral apex (F) on which three gynoecial appendages have been initiated (arrowheads). Some of the stamen and tepal primordia have been removed, X144. 22. Top view of the three gynoecial appendages (G) and site of ovule formation, X162. 23. Top view of an older stage showing young ovule primordium (O) surrounded by the three gynoecial appendages (G), X162. 24. Top view of a young gynoecium where the lower gynoecial appendage (G) has been moved to show the central ovule primordium (O), X162. 25. Same gynoecium as that of Fig.24 with lower appendage removed completely (rG) to show that the ovule primordium is not borne on any of the three gynoecial appendages, X162. 26. Top view of an older gynoecium showing upgrowth below the appendages as evidenced by regular cell files, X162. 27. Top view of young ovule with developing inner and outer integuments, X162.

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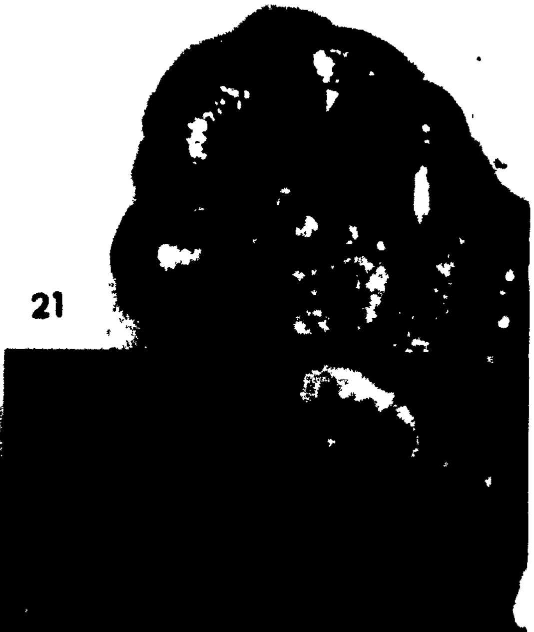

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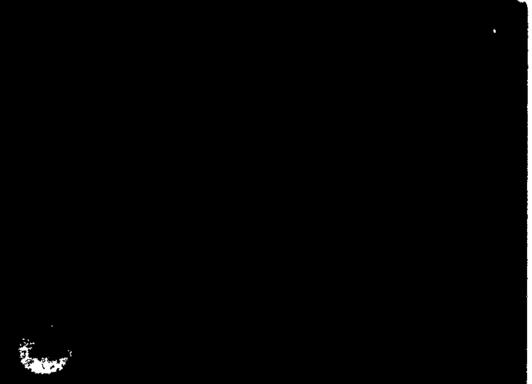

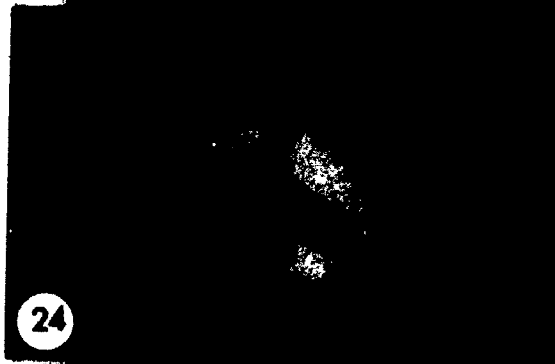

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Fig.28-30. Epi-illumination photographs of the young gynoecium and ovule. 28. Top view of the inside of the gynoecium at the base. The ovule (rO), at a slightly older stage of development than that of Fig.27, has been removed to show the early formation of septa (arrowheads) and locules, X84. 29. Side view of a gynoecium showing two of the three stigmas (Si). The short common style will form below (arrowhead), X74. 30. Side view of the ovule of a gynoecium at a stage similar to that of Fig.29. Note location of the micropyle (m) and the insertion of the ovule (arrowhead), X63.

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Fig.31-35. Longitudinal sections of different developmental stages of gynoecia in the adaxial-abaxial plane. 31. Nearly median section through the floral apex (F) showing the initiation of the adaxial gynoecial appendage through periclinal divisions below the outermost cell layer (arrowhead). Biv=involucral bract, A=stamen, X256. 32. Nearly median section showing the gradual transformation of the floral apex into the ovule. G=gynoecial appendage, X400. 33. Tunica-corpus organization still apparent in the ovule primordium (O), X256. 34. Older stage of gynoecial development. Periclinal divisions have occurred in the second cell layer of the ovule (O), X256. 35. Inner integument initiation through periclinal and anticlinal divisions (arrowheads) in the outermost cell layer and below, X224.

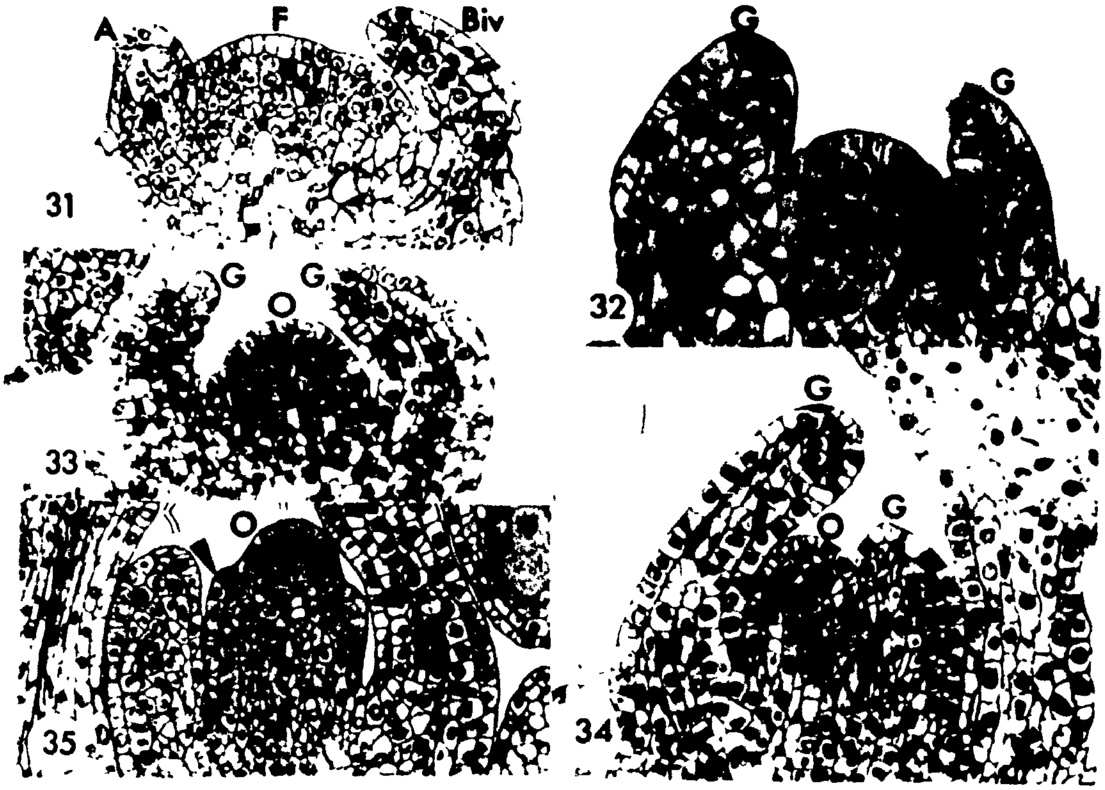
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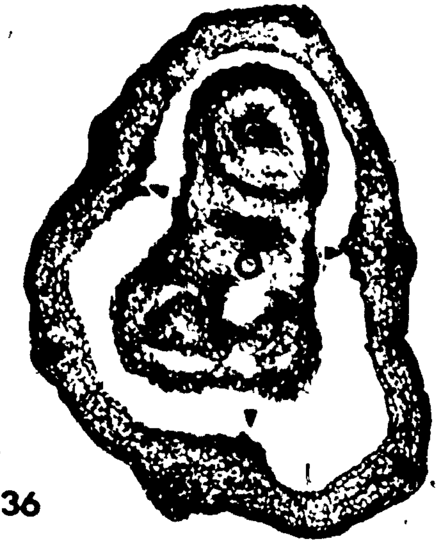
Fig.36-37. 36. Cross section through the gynoecium of a mature flower near its base showing the ovule (O) and beginning of partitions (arrowheads), X76. 37. Cross section of the base of the same gynoecium revealing the three locules (Lo), one of them slightly deeper than the other two. The micropylar end of the ovule (m) terminates in this particular locule, X76.

Fig.38-40. Cross sections of a nearly mature flower bud showing the vascular supply to the gynoecium. 38. Strands from major traces supplying the tepals and stamens (small arrows) merge to the center forming a ring (arrowheads), X76. 39. The vascular supply to the gynoecial wall is derived from this ring (arrowheads), X76. 40. The vascular supply to the ovule is also derived from this ring (arrowhead), X76. 41. Clearing of the base of a gynoecium showing anastamosing of strands (arrowhead) to form the single strand to the ovule (O). The arrow points to a strand unrelated to the gynoecium, X63.



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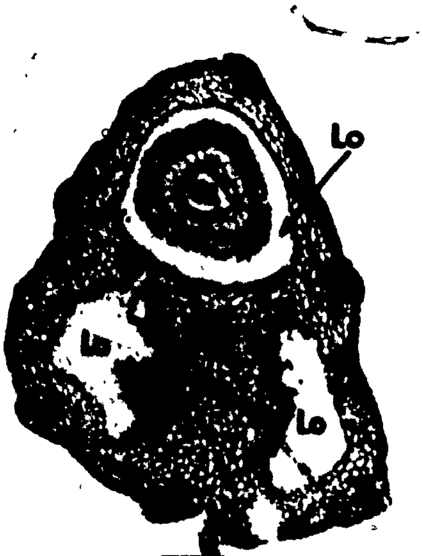

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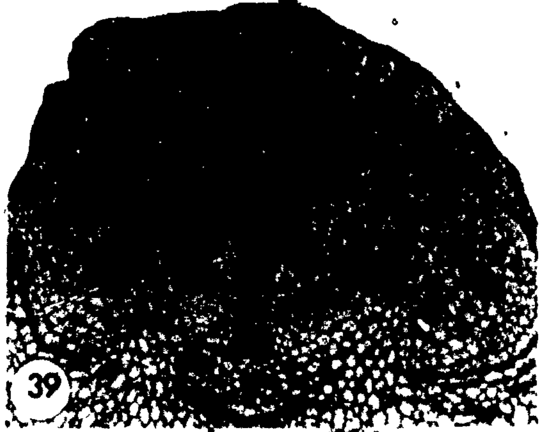

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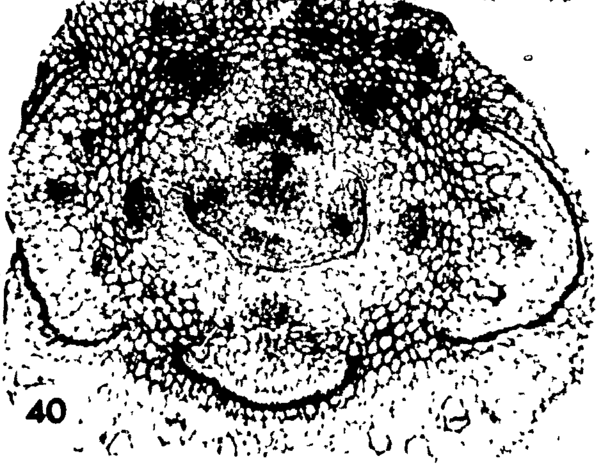

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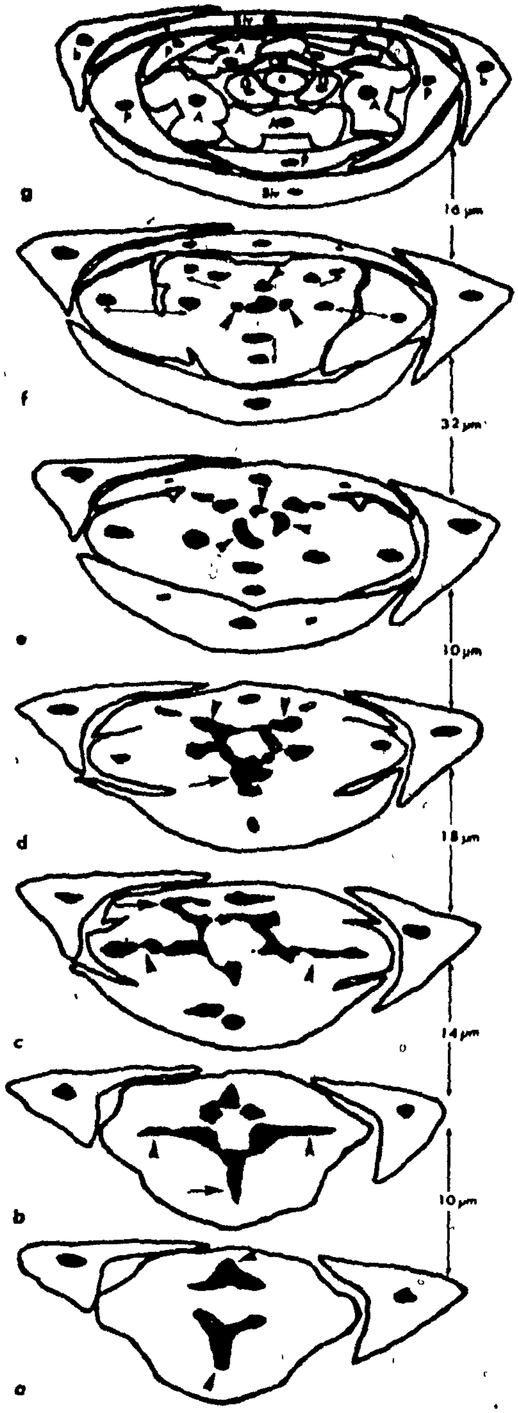
Fig.42. Selected drawings of serial cross sections through a nearly mature flower showing the vascular supply from the bottom (a) up (g). Subtending bract not included, X18. a. Supply to the involucral bracts (arrowheads). b=bracteoles. b-c. Branching of strands that supply tepals and stamens toward the abaxial side (arrowheads) and the involucral bracts (arrows). d. Branching of strands to tepals and stamens toward the adaxial side (arrowheads) and the abaxial tepal and stamen (arrow). e. Nearly circular central supply to the gynoecium (arrowheads). f. Tepal and superposed stamen strands originating as one at a lower level are separate at this level (double arrows). The supply to the gynoecium derives from the pattern in e. and consists of three strands (arrowheads) and a central supply to the ovule at this level. g. Level at which the flower parts and their vascular supply can be distinguished from each other. A=stamen; P=tepal; G=gynoecial appendage; O=ovule; Biv=involucral bract; b=bracteoles.


Sv
A
P
A
A
P
P
Sv
g
16 µm
f
32 µm
e
10 µm
d
18 µm
c
14 µm
b
10 µm
a

APPENDIX I

Classification of Angiosperms

legend: S= superposition; B= basal placentation
?= uncertain; fl.= flower

DICOTYLEDONAE (sensu Dahlgren, 1983)

1. MAGNOLIIFLORAE (9 orders, 23 families)
ANNONALES-
Annonaceae
Myristicaceae
Eupomatiaceae
Austrobaileyaceae
Cannellaceae
ARISTOLOCHIALES-
Aristolochiaceae
RAFFLESIALES-
Rafflesiaceae
including: Cytinaceae
Mitrastemonaceae
Hydnoraceae S
MAGNOLIALES-
Winteraceae
Degeneriaceae
Himantandraceae
Magnoliaceae
LACTORIDALES-
Lactoridaceae
NELUMBONALES-
Nelumbonaceae
CHLORANTHALES-
Chloranthaceae
ILLICIALES-
Illiciaceae
Schisandraceae
LAURALES-
Amborellaceae
Trimeniaceae
Monimiaceae
including: Siparunaceae B
Atherospermataceae
Gomortegaceae
Calycanthaceae
including: Idiospermaceae B
Lauraceae
including: Hernandiaceae S
Gyrocarpaceae

2. NYMPHAEIFLORAE (2 orders, 5 families)

PIPERALES-
Saururaceae
Piperaceae
including: Peperomiaceae B
NYMPHAEALES-
Cabombaceae
Ceratophyllaceae
Nymphaeaceae
including: Barclayaceae

3. RANUNCULIFLORAE (2 orders, 10 families)

RANUNCULALES-
Lardizabalaceae S
Sargentodoxaceae S ♂ fl.
Menispermaceae S
Kingdoniaceae
Circaeateraceae
Ranunculaceae
including: Hydrastidaceae
Glaucidiaceae pos. unc. related to Paeoniaceae
Berberidaceae B / S
including: Leonticaceae
Podophyllaceae
Nandinaceae
PAPAVERALES-
Papaveraceae
Fumariaceae
including: Hypecoaceae

4. CARYOPHYLLIFLORAE (1 order, 14 families)

CARYOPHYLLALES-
Phytolaccaceae
including: Achatocarpaceae B
Agdestidaceae
Limeum
Stegnospermataceae
Basellaceae B / S
Portulacaceae B / S
Hectorellaceae
Nyctaginaceae B
Aizoaceae
including: Tetragoniaceae B some
Mesembryanthemaceae
Halophytaceae
Chenopodiaceae B / S
including: Dysphaniaceae
Didiereaceae B
Cactaceae B some
Amaranthaceae B / S
Molluginaceae
Caryophyllaceae S ?
including: Illecebraceae

5. POLYGONIFLORAE (1 order, 1 family)

POLYGONALES-
Polygonaceae B

6. PLUMBAGINIFLORAE (1 order, 2 families)

PLUMBAGINALES-
Limoniaceae
Plumbaginaceae B/S

7. MALVIFLORAE (6 orders, 28 families)

MALVALES-
Sterculiaceae
Elaeocarpaceae
Plagiopteraceae
Bixaceae
Cochlospermaceae
Cistaceae
Sphaerosepalaceae pos. unc.
Sarcolaenaceae
Huaceae B
Tiliaceae
Dipterocarpaceae
Malvaceae B
Bombacaceae
URTICALES-
Ulmaceae S] apetalous
Moraceae S
Cecropiaceae B
Barbeyaceae
Cannabaceae S] apetalous
Urticaceae B/S
EUPHORBIALES-
Euphorbiaceae
including: Picrodendraceae
Hymenocardiaceae
Uapacaceae
Simmondsiaceae
Pandaceae
Aextoxicaceae pos. unc.
Dichapetalaceae
THYMELEALES- pos.unc.-
Thymelaeaceae
Gonystylidaceae distinct?
RHAMNALES-
Rhamnaceae B
ELAEAGNALES-
Elaeagnaceae B

8. VIOLIFLORAE (6 orders, 24 families)

VIOLALES-
Flacourtiaceae
including: Lacistemaceae
Passifloraceae

Dipentodontaceae
Peridiscaceae pos. unc.
Scyphostegiaceae B
Violaceae
Turneraceae
Malesherbiaceae
Achariaceae
Caricaceae
CUCURBITALES-
Datiscaceae S
Begoniaceae
Cucurbitaceae
SALICALES-
Salicaceae
TAMARICALES-
Tamaricaceae B
Frankeniaceae
CAPPARALES-
Capparaceae
including: Cleomaceae
Pentadiplandraceae
Koeberliniaceae
Brassicaceae
Tovariaceae
Resedaceae
Gyrostemonaceae
Batidaceae
Moringaceae S ?
SALVADORALES-pos. unc.
Salvadoraceae B

9. THEIFLORAE (3 orders, 20 families)

DILLENIALES-
Dilleniaceae
PAEONIALES-
Paeoniaceae
THEALES- a dubiously homogeneous order
Stachyuraceae
Pentaphylacaceae pos. unc.
Marcgraviaceae
Quiinaceae
Ancistrocladaceae
Dioncophyllaceae
Nepenthaceae
Medusagynaceae pos. unc.
Caryocaraceae
Strasburgeriaceae
Ochnaceae B
Oncothecaceae
Scytopetalaceae pos. unc.
Lecythidaceae
including: Asteranthaceae B
Foetidiaceae

Barringtoniaceae
Napoleonaceae
Theaceae
including: Tetrameristaceae
Pelliceriaceae
Bonnetiaceae
Clusiaceae
including: Hypericaceae B
Elatinaceae

10. PRIMULIFLORAE (2 orders, 9 families)

PRIMULALES-
Myrsinaceae B / S
Aegicerataceae B rarely / S
Theophrastaceae B / S
Primulaceae S
Coridaceae distinct?
EBENALES-
Sapotaceae B rare / S
Styracaceae
Lissocarpaceae
Ebenaceae the order dubiously homogeneous

11. ROSIFLORAE (15 orders, 44 families)

TROCHODENDRALES-
Trochodendraceae
Tetracentraceae S apetalous
CERCIDIPHYLLALES-
Cercidiphyllaceae
Eupteleaceae
HAMAMELIDALES-
Hamamelidaceae
including: Rhodoleiaceae
Altingiaceae
Platanaceae
Myrothamnaceae
GEISSOLOMOMATALES-
Geissolomataceae
BALANOPALES-
Balanopaceae
FAGALES-
Fagaceae
Corylaceae
Betulaceae S apetalous
JUGLANDALES-
Rhoipteleaceae
Juglandaceae B
MYRICALES-
Myricaceae B
CASUARINALES-
Casuarinaceae
BUXALES-
Buxaceae S

Didymelaceae
Daphniphyllaceae
CUNONIALES-
Cunoniaceae
Baueraceae
Brunelliaceae S ?
Davidsoniaceae
Eucryphiaceae
Bruniaceae
Grubbiaceae
SAXIFRAGALES-
Saxifragaceae
including: Penthoraceae S ?
Vahliaceae
Francoaceae
Brexiaceae
Grossulariaceae
Greyiaceae S ?
Iteaceae
Cephalothaceae B
Crassulaceae
DROSERALES-
Droseraceae B placenta
Lepuropetalaceae
Parnassiaceae
GUNNERALES-
Gunneraceae
ROSALES-
Rosaceae
Malaceae = (Pomaceae)
Amygdalaceae
Neuradaceae
Crossomataceae pos. unc.
Surianaceae pos.. unc.
including: Stylobasiaceae
Rhabdodendraceae pos. unc. B

12. PODOSTEMIFLORAE (1 order, 1 family)
PODOSTEMALES-
Podostemaceae
including: Tristichaceae

13. PROTEIFLORAE (1 order, 1 family)
PROTEALES-
Proteaceae S ?

14. MYRTIFLORAE (4 orders, 17 families)
HALORAGALES-
Haloragaceae
RHIZOPHORALES-
Rhizophoraceae S
MYRTALES-
Psiloxylaceae

Heteropyxidaceae
Myrtaceae
Onagraceae
Trapaceae
Lythraceae
including: Sonneratiaceae
Punicaceae
Alzateaceae
Combretaceae S ?
Melastomataceae B / S seldom
Memecylaceae
Crypteroniaceae
Rhynchocalycaceae
Oliniaceae
Penaeaceae
CHRYSOBALANALES-
Chrysobalanaceae

15. FABIFLORAE (1 order, 3 families)

FABALES-
Mimosaceae
Caesalpiniaceae
Fabaceae

16. RUTIFLORAE (6 orders, 46 families)

SAPINDALES-
Coriariaceae
Anacardiaceae
including: Pistaceaceae B some
Julianiaceae
Podoaceae
Leitneriaceae alt. in Rutales
Sapindaceae
Hippocastanaceae
Aceraceae
Akaniaceae
Bretschneideraceae pos. unc.
Emblingiaceae
Staphyleaceae
Melianthaceae
Sabiaceae S
Meliosmaceae
Connaraceae
RUTALES-
Rutaceae
including: Flindersiaceae
Ptaeroxylaceae
Cneoraceae
Simaroubaceae B some
including: Irvingiaceae
Tepuianthaceae
Burseraceae S ?
Meliaceae

including: Aitoniaceae
POLYGALALES- possibly heterogeneous
Malpighiaceae
Trigoniaceae
Vochysiaceae
Polygalaceae
including: Xanthophyllaceae
Diclidantheraceae
Krameriaceae pos. unc.
GERANIALES-
Zygophyllaceae S ?
Nitrariaceae
Peganaceae
Balanitaceae
Erythroxylaceae
Humiriaceae S ?
Linaceae
Ctenolophonaceae
Ixonanthaceae
Leipidobotryaceae S
Oxalidaceae
including: Averrhoaceae
Geraniaceae
Vivianiaceae
Ledocarpaceae
Biebersteiniaceae
Dirachmaceae
BALSAMINALES-
Balsaminaceae
TROPAEOLALES- alt. near Capparales
Limnanthaceae B
Tropaeolaceae

17. BALANOPHORIFLORAE (1 order, 2 families)

BALANOPHORALES- pos. unc.
Cynomoriaceae
Balanophoraceae S

18. SANTALIFLORAE (3 orders, 13 families)

CELASTRALES-
Celastraceae
including: Hippocrateaceae
Tripterygiaceae
Siphonodontaceae
Goupiaceae
Lophopyxidaceae
Stackhousiaceae
Cardiopteridaceae pos. unc.
Corynocarpaceae pos. unc. S
VITALES-
Vitaceae
including: Leeaceae B / S
SANTALALES

Olacaceae
including: Octoknemataceae] S
Opiliaceae B / S
Loranthaceae S
Misodendraceae
Eremolepidaceae S
Santalaceae B / S
Viscaceae S ♂ fl.

19. ARALIIFLORAE (2 orders, 5 families)

PITTOSPORALES-
Pittosporaceae
Tremandraceae pos. unc.
Byblidaceae pos. unc.
ARALIALES-
Araliaceae
Apiaceae

20. ASTERIFLORAE (2 orders, 4 families)

CAMPANULALES-
Pentaphragmataceae
Campanulaceae
including: Sphenocleaceae
Lobeliaceae
ASTERALES-
Asteraceae B

21. SOLANIFLORAE (2 orders, 12 families)

SOLANALES-
Solanaceae
including: Nolanaceae
Duckeodendraceae
Goetzeaceae
Sclerophylaceae
Convolvulaceae
including: Humbertiaceae] B
Cuscutaceae
Cobaeaceae
Polemoniaceae
BORAGINALES-
Hydrophyllaceae
Ehretiaceae
Boraginaceae
including: Wellstediaceae
Lennoaceae pos. unc.
Hoplestigmataceae pos. unc.

22. CORNIFLORAE (6 orders, 50 families)

FOUQUIERIALES-
Fouquieriaceae
ERICALES-
Actinidiaceae
including: Saurauiaceae

Clethraceae
Cyrillaceae
Ericaceae
Empetraceae
Monotropaceae
Pyrolaceae
Epacridaceae
Roridulaceae
Diapensiaceae
EUCOMMIALES-
Eucommiaceae
SARRACENIALES-
Sarraceniaceae
DIPSACALES-
Valerianaceae
Triplostegiaceae
Dipsacaceae
Morinaceae
Calyceraceae
CORNALES-
Garryaceae
Alangiaceae
Nyssaceae
Davidiaceae
Cornaceae
Helwingiaceae
Torricelliaceae
Aucubaceae
Aralidiaceae
Montiniaceae incl. Melanophylla
Escalloniaceae
Cardiopteridaceae
Phellinaceae
Aquifoliaceae
Sphenostemonaceae
Paracryphiaceae
Symplocaceae
Icacinaceae
Columelliaceae
Stylidiaceae
including: Donatiaceae
Alseuosmiaceae
Anisophylleaceae
Hydrangeaceae
Viburnaceae
Sambucaceae
Caprifoliaceae
Adoxaceae
position uncertain
Dulongiaceae
Tribelaceae
Eremosynaceae
Pterostemonaceae

Tetracarpaeaceae

23. LOASIFLORAE (1 order, 1 family)
LOSALES-
Losaceae S antepetalous stamen bundles

24. GENTIANIFLORAE (3 orders, 12 families)
GOODENIALES-
Goodeniaceae
including: Brunoniaceae
OLEALES-
Oleaceae
GENTIANALES-
Desfontainiaceae
Loganiaceae
including: Antoniaceae
Spigeliaceae
Strychnaceae
Potaliaceae
Dialypetalanthaceae
Rubiaceae
including: Henriqueziaceae
Menyanthaceae
Gentianaceae
Saccifoliaceae
Apocynaceae
Asclepiadaceae
Theligonaceae B

25. LAMIIFLORAE (4 orders, 20 families)
SCROPHULARIALES-
Bignoniaceae
Myoporaceae
Gesneriaceae
Buddlejaceae
Scrophulariaceae
including: Orobanchaceae
Globulariaceae
Selaginaceae
Stilbaceae
Retziaceae
Plantaginaceae B some
Lentibulariaceae B placenta
Pedaliaceae
Trapellaceae
Martyniaceae
Acanthaceae
including: Nelsoniaceae
Thunbergiaceae
Mendonciaceae
HIPPURIDALES-
Hippuridaceae
LAMIALES-

Verbenaceae
including: Phrymaceae
exclude Stilbaceae
Lamiaceae
Callitrichaceae
HYDROSTACHYALES- pos. unc.
Hydrostachyaceae

MONOCOTYLEDONEAE (sensu Dahlgren, 1985)

26. ALISMATIFLORAE (2 orders, 13 families)
ALISMATALES-
 Butomaceae
 Hydrocharitaceae
 including: Thalassiaceae
  Halophilaceae
 Aponogetonaceae
 Alismataceae
 Limnocharitaceae
NAJADALES-
 Scheuchzeriaceae
 Juncaginaceae
 including: Lilaeaceae
 Najadaceae B
 Potamogetonaceae] S
 including: Ruppiaceae] S
 Zosteraceae
 Posidoniaceae
 Cymodoceaceae
 Zannichelliaceae

27. TRIURIDIFLORAE (1 order, 1 family)
TRIURIDALES-
 Triuridaceae B

28. ARIFLORAE (1 order, 2 families)
ARALES-
 Araceae S
 Lemnaceae B

29. LILIIFLORAE (6 orders, 44 families)
DIOSCOREALES-
 Dioscoreaceae
 including: Stenomeridaceae
 Trichopodaceae
 Taccaceae
 Stemonaceae B
 including: Croomiaceae
 Trilliaceae
 Smilacaceae
 Petermanniaceae
BURMANNIALES-
 Burmanniaceae S] when 3 stamens
 Thismiaceae S] when 3 stamens
 Corsiaceae
ORCHIDALES-
 Apostasiaceae
 Orchidaceae
 Cypripediaceae
ASPARAGALES-
 Philesiaceae

Luzuriagaceae
Convallariaceae
Asparagaceae
Ruscaceae
Herreriaceae
Asteliaceae
Dracaenaceae
Nolinaceae
Hanguanaceae
Agavaceae
Dasypogonaceae
Calectasiaceae
Blandfordiaceae
Xanthorrhoeaceae
Hypoxidaceae
Tecophilaeaceae
Ixioliriaceae
Cyanastraceae
Dianellaceae
Phormiaceae
Doryanthaceae
Eriospermaceae
Asphodelaceae
including: Aloeceae
Anthericaceae
Aphyllanthaceae
Hemerocallidaceae
Funkiaceae
Hyacinthaceae
Alliaceae
including: Agapanthaceae
Gilliesiaceae
Amaryllidaceae
LILIALES-
Colchicaceae
Uvulariaceae
Iridaceae
Geosiridaceae
Alstroemeriaceae
Liliaceae
Calochortaceae
MELANTHIALES-
Melanthiaceae
Campynemaceae

30. BROMELIIFLORAE (6 orders, 7 families)

VELLOZIALES-
Velloziaceae
BROMELIALES-
Bromeliaceae S
HAEMODORALES-
Haemodoraceae S
PHILYDRALES-

Philydraceae S
PONTEDERIALES-
Pontederiaceae
TYPHALES-
Sparganiaceae S
Typhaceae

31. ZINGIBERIFLORAE (1 order, 8 families)
ZINGIBERALES-
Lowiaceae S
Musaceae
Heliconiaceae
Strelitziaceae
Zingiberaceae B
Costaceae
Cannaceae
Marantaceae

32. COMMELINIFLORAE (4 orders, 17 families)
COMMELINALES-
Mayacaceae
Commelinaceae
including: Cartonemataceae
Xyridaceae S
with hesitation Abolbodaceae
Rapateaceae
Eriocaulaceae
HYDATELLALES-
Hydatellaceae pos. unc.
CYPERALES-
Juncaceae B
Thurniaceae
Cyperaceae B
POALES-
Flagellariaceae
Joinvilleaceae
Poaceae B
Ecdeiocoleaceae
Anarthriaceae
Restionaceae S
Centrolepidaceae

33. ARECIFLORAE (3 orders, 3 families)
ARECALES-
Arecaceae B placenta
CYCLANTHALES-
Cyclanthaceae S staminodes-tepals ♀ fl.
PANDANALES-
Pandanaceae

approximate frequency (dicots): B=12% - S=14%
approximate frequency (monocots): B=8% - S=13%
approximate frequency (Angiosperms): B=11% - S=13%